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PALAEOONTOLOGY

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CORRIGENDA

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- page 155, line 18: For 'GSM 7176', read 'GSM 7177'.
page 155, line 5 up: For 'GSM 87097', read 'GSM 87079'.
page 163, line 8: For 'GSM 7176', read 'GSM 7177'.
page 164, line 7: For 'Plate 26, fig. 11', read 'Plate 26, fig. 10'.
page 164, Explanation of Plate 26,
 line 5 up: For 'Fig. 10', read 'Fig. 11'.
 line 4 up: For 'GSM 7176', read 'GSM 7177'.
 line 3 up: For 'Fig. 11', read 'Fig. 10'.
page 182, Explanation of Plate 29,
 line 6 up: For 'GSM 87091', read 'GSM 87101'.
page 227, line 12 up: For 'Muscovian', read 'Moscovian'.
page 240, Explanation of Plate 41,
 line 3 up: For 'partition', read 'extremity'.

ABNORMAL GROWTHS IN SOME DEVONIAN GONIATITES

by MICHAEL R. HOUSE

ABSTRACT. Specimens of *Sobolewia* from the Givetian of Cornwall and Algeria are described which show a regular pitting on the internal moulds. The same phenomenon is noted on an Algerian Eifelian goniatite and also on German specimens of *Sellanarcestes* from the Emsian and Eifelian and on an Eifelian *Anarcestes*. The pits, which are commonly arranged in sub-radial rows, are interpreted as formed in life as mound-like growths on the side of the anterior part of the body chamber shell, but not along the apertural margin. Several hypotheses on their origin are discussed.

THE curious pitting seen on the internal moulds of some Devonian goniatites which is here described was first observed on specimens of *Sobolewia* from the locality described by Fox (1894, p. 637) at Pentonwarra Point, Trevone, north Cornwall. The fauna here has recently been shown to belong to the Terebratulum Zone of the Middle Devonian Maenioceras Stufe and not to the Upper Devonian as had hitherto been supposed (House 1956). The goniatite genera now known from this locality include *Tornoceras*, *Aulatornoceras*, *Protornoceras*, *Maenioceras*, *Sobolewia*, *Agoniatites*, *Wedekindella*, and *Werneroceras*, but only certain specimens of *Sobolewia* show the pitting.

During April 1957 a period was spent in Paris examining the superb collections of Devonian ammonoids from North Africa at the Sorbonne. Discussion with Madame Germaine Petter of the Centre de Recherches Sahariennes revealed that many Saouran specimens of *Sobolewia* show the pitting as does one Eifelian specimen. In August 1958, whilst studying the ammonoid collections in the Geologisch-Paläontologisches Institut at Göttingen, one Emsian goniatite was noted showing pits. Later, at the Geol.-Paläontologisches Institut at Marburg, Dr. O. H. Walliser was able to show the writer several Middle Devonian specimens which also showed pitting.

Special thanks are due to Madame Petter for discussion in Paris and for reading and commenting on the typescript and to Professor Pierre Pruvost for providing facilities for study at the Sorbonne. Dr. Herman Schmidt and Dr. Otto H. Walliser are also to be thanked for discussion and for making specimens available for study. In an unsuccessful attempt to discover whether such pits occurred on the moulds of ammonoids of other periods the matter was discussed, in person or by correspondence, with most leading specialists. Acknowledgement is due especially to Mr. W. S. Bisat and to the late Dr. V. J. Arkell. Also appreciated are the comments of Dr. Otto Haas, Professor F. Hodson, and Dr. G. A. L. Johnson. The Durham Colleges in the University of Durham have given grants to facilitate travel in Europe in the course of monographic work on the English Devonian ammonoids. Mr. C. Chaplin of the Durham Colleges, Dr. Walliser of Marburg, and Mr. Jack Scott of the U.S. National Museum in Washington have given help in the preparation of the accompanying photographs.

DESCRIPTION

Cornish specimens. The specimens of *Sobolewia* from Trevone are preserved as internal moulds of iron pyrites with occasional pyritic casts of the original shell. Pitting has been

seen on specimens between 8 mm. and 21 mm. diameter and it occurs on septate portions of the moulds and on at least the posterior portions of the body chamber. Not all specimens of *Sobolewia* show the pitting and some show only occasional development of pits.

The pits range between 0.3 mm. and 0.9 mm. in diameter and their sides slope convexly inward to form a sub-conical depression which may reach 0.5 mm. in depth. Where observed the pit bottom is rounded. The outer margin of the pits grade even-



FIG. 1

TEXT-FIG. 1. *Sobolewia* aff. *nuciformis* (Whidborne). *a*, Course of growth lines. *b*, Approximate course of pit rows (variable over the umbilico-lateral areas). *c*, Suture. Scale in millimetres. All based on SM H7422 collected by the author from the Terebratrum Zone, Givetian, at Pentonwarra Point, Trevone North Cornwall.



FIG. 2

TEXT-FIG. 2. *Sellanarcestes* cf. *wenkenbachi* (Kayser). Diagram showing one suture and the distribution of pitting on a specimen in the Göttingen Geologisch-Paläontologisches Institut from the Emsian Mandelner Schichten at Mandeln, Germany. The dotted line shows a hypothetical arrangement of the pits into rows. Each scale division represents approximately 5 millimetres.

into the internal mould of the shell. The relation of the pits to the shell has been elucidated in one instance by the dissection of an undisturbed pyritic cast of the shell from above a pit. The outer surface of the shell showed no evidence of disturbance. Pits formed on the moulds of mural areas of the septa show no difference from those found elsewhere. Occasionally two or more pits may partly coalesce.

In some specimens the pits occur rarely and it is not possible to distinguish any regular arrangement of them. In several specimens, however, the pits are seen to be arranged in rows which pass out from the umbilicus, cross the lateral areas either radially or with a slight forward projection, and on the ventro-lateral slopes pass back to form a shallow and narrow sinus on the venter (text-fig. 1*b*). In some specimens there are five to eight of these rows in a half whorl with about five pits between the umbilicus and the venter. There is approximately an equal development of pits on either side, but the pits are not symmetrically placed. The pit arrangement between successive rows does not show precise agreement. The distance between the rows agrees in general with the distance between the septa. The rows do not agree with the course of the growth lines (text-fig. 1*a*, *b*, Pl. 24, fig. 5) at the same diameter, nor do they correspond with the course of growth lines for one whorl or ad of the pit rows.

North African specimens. Specimens of *Sobolewia* in the Sorbonne from the Givetian of the Redjel Imrad collected by J. Fallot show pitting on the internal moulds exact-

comparable with that described for Cornish specimens. In no specimen is there any trace of the original shell. Other genera from the same locality show no pitting.

A single specimen from the southern border of the Erg el Djemel (Ougarta) from the Eifelian 'niveau à *Pinacites jugleri*' shows the pitting in a remarkable way (Pl. 24, fig. 6). This specimen is unfortunately not generically determinable since it is crushed laterally and the sutures cannot be seen. The specimen is 20.4 mm. in diameter and at least the last whorl represents the body chamber. Pitting can be observed on the right side of the specimen, but that side is poorly preserved. The figured left side shows no orderly arrangement of pits in the apicad portion of the body chamber, but in the subsequent whorl they become almost invariably arranged into forwardly projecting slightly concave rows with some suggestion of a backward deflexion over the venter. There is a noticeable absence of pits on the umbilical shoulder: between the shoulder and the venter there are usually between eight and ten pits. Ventro-laterally the pit arrangement is disturbed and although there is some indication of a backward deflexion to form a sinus there are many pits which do not follow this regular course. Except in a few cases there is not complete agreement in the position of pits in successive rows. Whilst the pits are usually of the same size they occasionally coalesce and there are some smaller pits. The small particles seen within many of the larger pits are pyritic concretionary structures. Growth-lines are not well shown on the specimen but in the early portion of the last whorl there is evidence that they sweep very slightly back from the umbilicus to form a very shallow sinus on the outer flanks: their course over the venter cannot be discerned.

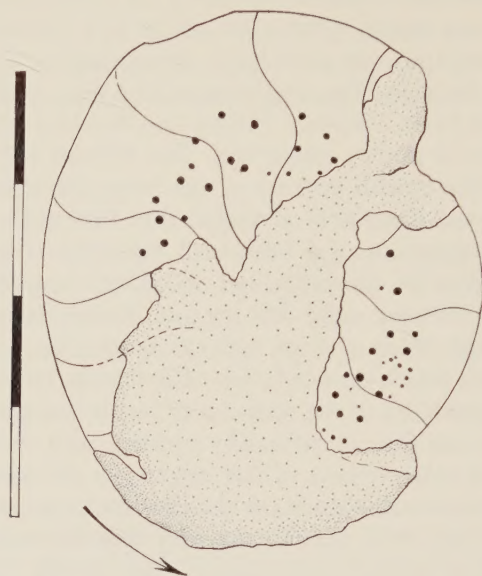
German specimens. One specimen of *Anarcestes* sp. in the Clausthal Museum (No. L 62) from the Upper Eifelian Goslarer Schiefer (Pl. 24, fig. 7) shows a pattern of pitting which is closely comparable to that seen on the Cornish and Algerian specimens. Again the pits are apparently arranged into sub-radial rows with some evidence of a ventral sinus. The separation between the rows in this case does not agree with the septal separation at the same diameter, but it may agree with the septal separation at earlier diameters which cannot be seen. The pit arrangement is not laterally symmetrical.

There is a specimen in the Geol.-Pal. Museum at Berlin (No. c104) from the Eifelian Ballersbacher Kalk at Blauer Bruch near Wildungen which Dr. O. H. Walliser has determined as *Sellanarcestes* cf. *wenkenbachi* (Kayser) (Pl. 24, figs. 8, 9) which shows pitting with a different arrangement to that so far described. Although there is a radial pattern there are fewer pits and these appear to be spirally arranged and single prominent pits lie in a constant ventro-lateral position throughout the last whorl.

A specimen from the Upper Coblencian (Emsian) of Mandeln which Schmidt (1926, p. 293) figured and referred to '*Anarcestes wenkenbachi*' shows evidence of pitting (text-fig. 2). This specimen is in the Geol. Pal. Institut at Göttingen. In this example the pits are not frequent and are completely without symmetry in their arrangement, but they can be interpreted as arranged into a row which has a salient on the outer flanks and a concavity on the venter.

The most remarkable pitting is exhibited by a single specimen of *Anarcestes* (*A.*) sp. in the Clausthal Geol.-Pal. Institut from the Eifelian Wissenbacher Schiefer (text-fig. 3). In this case the pitting is restricted to a broad band low on the flanks. There is no evidence to suggest any radial arrangement of the pits at all. Further, the pits are not

of uniform size, and very small pits occur among pits of similar size to those found in the forms already described.



TEXT-FIG. 3. *Anarcestes (Anarcestes) sp.* Lateral view of a specimen in the Clausthal Museum labelled '*Anarcestes vittatus*' from the Eifelian Wissenbacher Schiefer showing pits on the internal mould. The arrow shows the direction towards the aperture. Each scale division represents 5 millimetres. Based on drawings and a photograph and checked against the original specimen by Dr. O. H. Walliser of Marburg.

INTERPRETATION

The possibility that the pits are post-fossilization features is clearly ruled out in the case of *Sobolewia* by their relation to the shell and mural portions of the septa: these show that the pits were formed during life. In the other cases it is difficult to conceive how such regular pitting could have arisen accidentally. There is therefore no comparison with the pitting which has been described, for example, on the surface of the holotype of *Perisphinctes* (? *P.*) *listeri* (de Haan) from the Jurassic Corallian Beds of Nunnington, Yorkshire, which Dr. Vernon Wilson has suggested may be due to the subsequent action of rootlets and humic acid (*in* Arkell 1950, p. 265). The Cornish specimens described here have been extracted from freshly exposed and unweathered intractable slate.

From the preceding description and observations the following inferences on the origin of the pits may be made.

1. The pits are moulds of mounds which were developed during life on the inner surface of the shell.
2. The mounds were probably solid since mural portions of the septa reflect their shape and iron pyrites subsequently formed around them.

3. The mounds were formed in the body chamber and near to the aperture, but were not formed along the shell-growth margin. Where there is a regular arrangement of the pits into rows the course of the rows does not agree with that of the growth lines.

4. At least in specimens other than the *Anarcestes* (*A.*) *sp.* from the Wissenbacher Schiefer, the arrangement of the pits into rows which agree approximately in their separation with the septal distance suggests that the mounds were formed periodically after each forward movement of the visceral mass associated with septal formation.

The several possible causes of the mounds will, for convenience, be discussed under three heads.

(1) *Functional mounds.* There are at least three known ammonoid structures with which the mounds may have been functionally associated: *a*, small muscle attachment; *b*, incipient false constrictions; *c*, modified conellae.

The evidence appears to tell against the mounds representing the site of small muscles. Were this the case it might be expected that the pit arrangement would be laterally symmetrical and that there would be nearly precise agreement between the position of the pits in successive rows. Further, it might be expected that all specimens of affected genera preserved as internal moulds would show the pitting, but this is not the case. However, a pitting on the interior of the posterior parts of the nautiloid body chamber has been illustrated in *Phragmoceras* by Foerste (1929) and Sweet (1959) has illustrated similar structures in the genera *Parryoceras*, *Beloitoceras*, *Oncoceras*, and *Diestoceras*. But in these cases the pitting is regular and restricted to a band immediately orad of the last septum. The pit rows in the Devonian goniatites are not comparable with the course of the annulus for Crick (1898) has shown that when this structure is shown on ammonoids it is still in the posterior part of the body chamber as in the living *Nautilus*.

The pits show little analogy with constrictions except that the course of the pit rows shows agreement with false constrictions in failing to accord with the growth lines, in being structures on the inside of the body chamber, and in their formation being near the aperture. The frequency of constrictions rarely, if ever, agrees with the septal frequency. No constrictions have been recorded in the Devonian genera affected by the pitting. Pit-like depressions on the lateral areas of the internal moulds of some ammonoids with constrictions do occur, however, and they are shown on *Dunbarites rectilateralis* (Miller) (see Miller and Furnish 1940, p. 532, pl. 63, figs. 1, 4), but there are never rows of pits as shown in some Devonian goniatites.

The mounds are not directly comparable with the conellae described within the shell of certain Jurassic ammonites (Hölder 1952; 1952*a*) for although these structures are conical their apices are directed outwards, whereas the apices of the mounds in the Devonian goniatites are directed inwards. Further, the relative size of conellae is much smaller than the mounds. Also conellae are usually interpreted as formed by diagenic dissolution of the shell, whereas the Devonian structures were clearly formed in life.

(2) *Alien organic growths.* Internal discrete alien organic growths might be expected to leave trace of a distinct boundary on the internal moulds. This is not seen on the Devonian specimens and in all cases the pits are in smooth continuity with the surrounding areas. The pits on the body chamber of *Manticoceras oxy* Clarke, refigured by Miller (1938, Pl. 16), were formed by orbiculoideans growing on the internal surface of the

body chamber and these show the distinct boundary to be expected from organic growths.

Borings through the shell from the outside are common among recent Mollusca and may give rise to internal mounds. Professor F. Hodson informs the writer that borings are not uncommon on the shells of Carboniferous goniatites and they are well shown on the holotype of *Hibernicoceras posthibernicum* Hodson and Moore (1958, pl. 4, fig. 1). Structures have also been figured by Schindewolf (1934, pl. 2, fig. 7a, b) as borings in the shell of a specimen of *Cymaclymenia striata* (Münster) from the Upper Devonian of Hönnetal, Germany. The pits in *Sobolewia* can hardly be due to borings since the shell above the pits is undisturbed. Whilst no trace of the shell is visible in the affected North African Eifelian specimen (SM. H 7423) the arrangement of the pits into periodic rows could only be explained as due to borings if some soft part structure extended fully onto the whorl beyond the aperture of the body chamber which is itself at least one whorl in length: it seems unlikely that this could be the case.

(3) *Localized shell thickenings*. The continuity between the pits and adjacent areas suggests that the mounds were tumorous concretions of actual shell material which formed after each advance of the body mass. Such tumorous growths might be due either to organic infection or inorganic irritation which led to the precipitation of actual shell material. In either case the resulting structures could be termed pathological (Moodie, 1923, p. 29). Were organic infection the cause it is surprising that the pits are usually so regular for, at times, the infection might be expected to disrupt the soft parts considerably. The possibility that the mounds might be caused by the irritation of permanent cysts or similar structures within the visceral mass is considered unlikely because of the lack of agreement in the position of the pits in successive rows.

An inorganically or organically caused irritation not primarily related to the shell or the soft parts seems a more likely solution. Small particles could conceivably enter between the shell and the visceral mass and lead to structures comparable with the pearl mounds of present-day lamellibranchs. The precise origin of natural pearls has been so disputed that attempts to deduce it for Devonian goniatites are unlikely to be profitable. Magraw (1956) has recently suggested that foreign particles may explain abnormal apertural developments in *Gastrioceras*. If a similar type of interpretation is correct for *Sobolewia* then the rows of mounds must be caused by some structure in the soft part

EXPLANATION OF PLATE 24

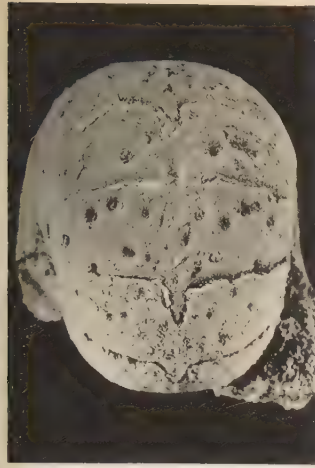
Figs. 1-5. *Sobolewia* aff. *nuciformis* (Whidborne). 1, SM. H7421 collected by the author from the Givetian Terebratum Zone at Pentonwarra Point, Trevone, north Cornwall. $\times 4$. 2-5, SM. H7422 collected by the author from the same locality and horizon. 2, 3×4 , 4×12 , 5×11 .

Fig. 6. Goniatite indet. SM. H7423 from the Eifelian 'niveau à *Pinacites jugleri*', Erg el Djemal (Ougarta), North Africa. $\times 3$.

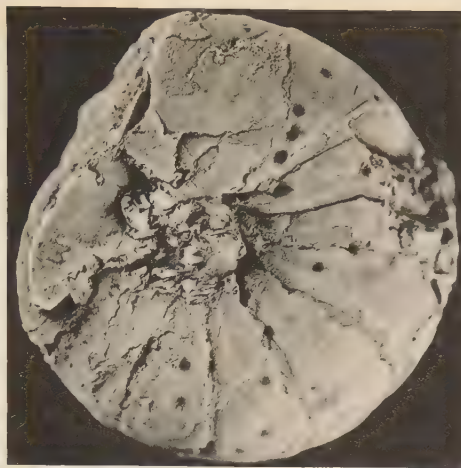
Fig. 7. *Anarcestes* sp. Clausthal Museum No. L.62 from the Upper Eifelian Goslarer Schiefer. $\times 4$.

Figs. 8, 9. *Sellanaercestes* cf. *wenkenbachi* (Kayser). Berlin Museum No. c104 from the Middle Couvinian (Eifelian) at Blauer Bruch near Wildungen. $\times 2$.

All the specimens are of natural internal moulds, but SM. H7422 retains a portion of the original shell preserved as a pyritic cast. The specimens were lightly coated with a sublimate of ammonium chloride before being photographed. The prefix SM. refers to the Sedgwick Museum collections where some of the figured specimens have been deposited.



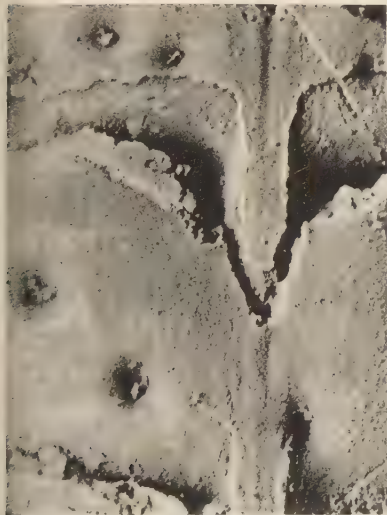
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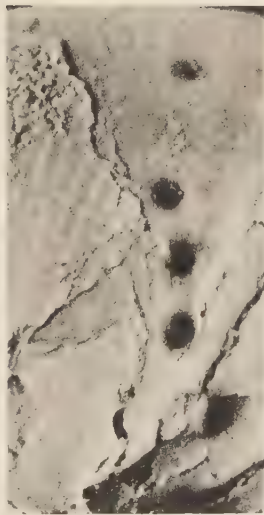
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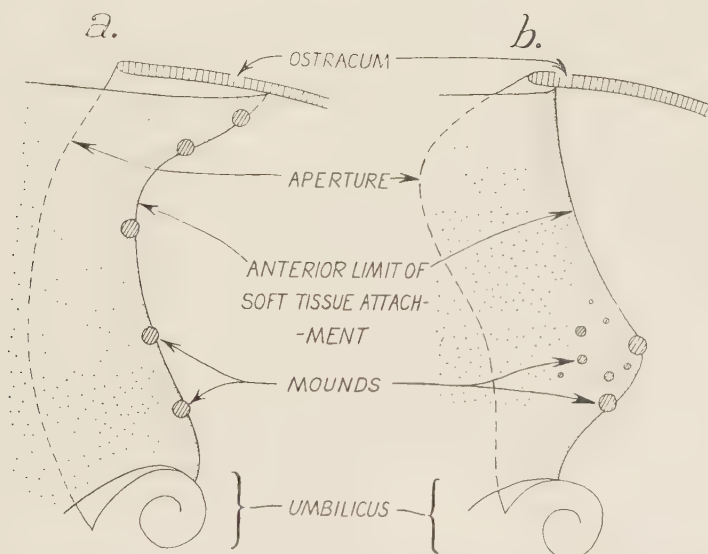


8



9

which limited the backward passage of foreign particles. Perhaps this structure might be the anterior limit of soft part attachment, comparable with the pallial line of the lamelli-branch. The restriction of the mounds to a band on the flanks could be explained by a lateral sinus along the 'pallial line' (text-fig. 4). This line, in other forms, might be the site of the precipitation of false constrictions. The wrinkle layer on Devonian goniatites commonly reaches near to the aperture and the striae of it do not follow the course of the wrinkle layer in the affected Devonian goniatites to tell whether the pit rows follow the same course.



TEXT-FIG. 4. Diagram showing a hypothetical relation between mounds and soft parts in a, *Sobolewia* and b, *Anarcestes*. Based on specimens described in the text.

CONCLUSIONS

The evidence at present available is not conclusive as to the origin of the pits seen on some Devonian goniatites, but appears to favour an hypothesis that the pitting is due to pearl-like mounds which were formed in life on the inside of the body chamber and probably caused by the irritation of foreign particles which entered between the body and the shell: the particles were apparently restricted in their passage backward by some unknown structure in the soft parts, possibly the anterior limit of soft part attachment. Periodic forward movement of the visceral mass associated with septal formation during growth then explains the arrangement of the pits into periodic rows the separation of which generally agrees with the septal distance. A sinus formed along the limit of soft part attachment could explain the restriction of the pits into a lateral band in some cases.

The genera in which this phenomenon has been observed are all members of the

Devonian family Anarcestidae with the possible exception of *Sobolewia* which is commonly placed in the Prolobitidae. Affected specimens occur in the Emsian, Eifelian, and Givetian. Occurrences are known in North Africa, Germany, and England.

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LOWER CARBONIFEROUS NON-MARINE LAMELLIBRANCHS FROM EAST FIFE, SCOTLAND

by G. M. BENNISON

ABSTRACT. *Carbonicola antiqua* Hind (*non* Brown) and *C. elegans* (Kirkby) are redescribed from the Calciferous Sandstone Series of East Fife, and *Anthraconaia? kirki* sp. nov. proposed. Variation of the shells at different localities is discussed and the significance of faunal associations is assessed.

THREE species of non-marine lamellibranch have been described from the Calciferous Sandstone Series (Lower Carboniferous) of East Fife. Of these, two were referred to *Carbonicola* and one to *Naiadites* by Hind (1894-6). Detailed work has shown that the two species of *Carbonicola* were correctly referred to that genus by Hind, and that they are morphologically more primitive than other representatives of the genus, as well as occurring at a lower horizon. Examples of *Anthraconaia?* are also described here. The strata from which the shells described are derived are of Viséan age (Currie 1954), and are extremely variable. They thin from about 4,000 feet on the coast of East Fife, to little more than 200 feet in the Lomond Hills 15 miles away. Rapid lateral thinning of individual beds, local unconformities cutting out parts of the succession, slumping of shales, and the lenticular form of the false-bedded, ripple-marked sandstones all show that deposition was in water shallow enough to be affected by currents or wave action. Occasional coal seams indicate temporary emergence. Lack of precise knowledge of the stratigraphy of the beds is a serious limitation to palaeontological study. Text-fig. 1 shows the localities mentioned.

Certain detailed correlations postulated by Kirkby cannot be sustained, though little can be suggested in their place. The Randerstone shore section is low in the Calciferous Sandstone Series—Kirkby equates his Limestone 5 with Bed 618 of the Pittenweem to Anstruther section—but it is doubtful if Limestone 10 is the equivalent of Bed 649. They differ in lithology and in fauna and form part of different successions. Nor can the postulated correlation of the beds with *C. antiqua* at Kilminning and Kilrenny Mill be upheld. Variation in the shells differs at these localities and the beds are lithologically distinct. Summarized detailed successions are as follows:

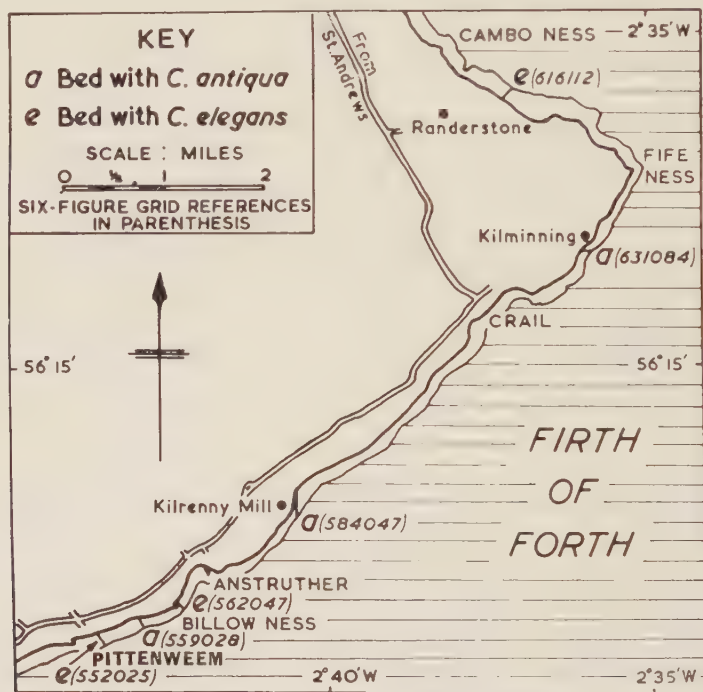
KILMINNING	KILRENNY MILL
10-12 ft. shale	8 ft. shales and sandstones
10 in. hard red limestone with abundant <i>C. antiqua</i>	3 in. cementstone
3 in. calcareous sandstone	5 in. mudstone with <i>C. antiqua</i>
+ 5 ft. massive sandstone	1 in. clay
	6-10 in. hard, yellow, calcareous sandstone with many <i>C. antiqua</i>
	4 ft. 9 in. sandy shale

CARBONICOLA IN THE LOWER CARBONIFEROUS

Lower Carboniferous *Carbonicola* differ from most Westphalian forms in having tilted growth lines. These reflect a progressive change in the direction of growth and

Palaeontology, Vol. 3, Part 2, 1960, pp. 137-152, pl. 25.]

result in low umbones directed towards the anterior in the adult shell. In some specimens the umbo is not the highest part of the dorsal margin. The postero-dorsal margin, which is typically arched, becomes strongly arched in some variants. The hinge is edentulous, a condition not typical in *Carbonicola*, although noted in the Namurian species *C. pervetusta* (Bennison 1954, p. 41). Further, Eagar (1946, p. 7), describing small forms from the *Anthraconaia lenisulcata* zone of the Coal Measures, has observed that teeth are ill defined and that dentition is represented mainly by swellings and depressions in the hinge-plate. Trueman and Weir (1951, p. 106) state that the edentulous condition occurs 'not infrequently' in *Carbonicola*: in this case it may be indicative of a primitive condition.



TEXT-FIG. 1. Sketch map to show the location of non-marine lamellibranch beds in east Fife.

Despite a superficial similarity to *Anthracosia*, due to the tilted growth lines and the low umbones, and, despite the vertical anterior umbonal slope of the internal mould, these *Carbonicola* are seen to differ fundamentally from *Anthracosia* in that the internal moulds do not have a robust median dorsal ridge. By implication, the hinge-plates cannot be bevelled as in *Anthracosia*. It is the structure of the dorsum which distinguishes *Anthracosia* from *Carbonicola* (Trueman and Weir 1951, p. 105), although 'the dorsal structure indirectly affects some aspects of external shape—e.g. umbonal tilt and outline of dorsal plan'. Thus in the Lower Carboniferous there are early members of the Anthracosiidae resembling *Carbonicola* in essential characters but bearing a superficial similarity to *Anthracosia*.

Carbonicola antiqua Hind

Plate 25, figs. 1, 2, 6-8

? Pachyodon nucleus Brown 1843, p. 394, pl. 16, fig. 1.*Carbonicola antiqua* Hind 1894, p. 79, pl. 11, figs. 28-30.Non *Carbonicola antiqua* (Brown); Trueman and Weir 1947.

Type material. The specimen figured by Brown as *Pachyodon nucleus*, from Woodhall, Water of Leith, near Edinburgh, is lost. I have studied faunas from Brown's type locality collected by Geological Survey officers, but found nothing with which *nucleus* could be identified. As the identity of Brown's species cannot be determined it is impracticable to sustain the name *nucleus*. Brown was correct (1849, p. 178, pl. 23, fig. 31) in renaming his Coal Measures form *Pachyodon antiquus* as *senex* on referring that species to the genus *Unio*, for the name *Unio antiquus* was preoccupied by Sowerby's (1833) species. The correct name for *C. antiqua* Brown, as used by Trueman and Weir (1947), is therefore *C. senex* (Brown). No homonymy occurs, however, in the case of *C. antiqua* Hind. Hind's specimens are syntypes and his first figured specimen (1894, pl. 40, fig. 28, B.M. L.46889) is here selected as lectotype.

Diagnosis. Shell ovate to subtriangular. Umbones low, anterior end short, *c.* 20 per cent. of the length or less. Growth lines tilted. Tumid, thickness over 40 per cent. of the length. Posterior bluntly rounded or obliquely truncated. Lower border gently rounded, or straight for the posterior two-thirds of its length.

Dimensions

	<i>L</i> (mm.)	<i>H</i> (mm.)	<i>A</i> (mm.)	<i>T</i> (mm.)
Pl. 25, fig. 1 (L.46889) (Hind, pl. 11, fig. 28)	24.0	14.5 (60.4%)	4.2 (18.3%)	est. 5.9 (single valve) (<i>c.</i> 49%)
Pl. 25, fig. 2 (L.46890) (Hind, pl. 11, fig. 29)	25.3	15.4 (60.9%)	4.5 (17.7%)	12.6 (49.6%)

Description and discussion. The syntypes are rather larger than the mean for the topotype material from Kilminning collected by the author, but the values for H/L and A/L are very close to the modes of the community. The lectotype is near the norm of the community and is typical in every way except in the detail of the posterior-umbonal slope, which is less strongly arched than in some variants, and the umbo, which is more pronounced than in the majority of adult specimens. The growth lines are only moderately tilted. The figured syntype represents a common variant with low umbones, highly tilted growth lines and a rather bluntly truncated posterior end. Variation in the community is discussed below. *C. antiqua* is edentulous and in no case have teeth or dental sockets been found; this is in accord with Hind's original description although his figured hinge-plate (1894, pl. 11, fig. 28*a*) does not provide clear evidence of this.

Comparison. *C. elegans* is the only other species of Lower Carboniferous lamellibranch which resembles *C. antiqua*. *C. elegans* occurs 250 feet below and 950 feet above *C. antiqua* and their ranges, though not fully known, must overlap. The two species do not occur together. They can be readily distinguished, chiefly on account of a large discrepancy in the value of H/L, and by features fully discussed in the emended description of *C. elegans*.

C. antiqua and *C. elegans* differ from *C. pervetusta*, the earliest form assigned to *Carbonicola* by the writer, in the following features: the umbones are low and directed towards the anterior; the growth lines are tilted; the shells are more tumid; the anterior end is short— $A/L = 20$ per cent. or less; the shells normally attain a greater size; and the range of variants is different.

Distribution. The syntypes are from red limestone at Kilminning, between Fife Ness and Crail. This species also occurs in two beds at Kilrenny Mill, and sparsely at a higher horizon between Pittenweem and Anstruther. It is restricted, therefore, to the lower part of the Calciferos Sandstone Series. The habitat of *C. antiqua* is discussed below.

Carbonicola elegans (Kirkby)

Plate 25, figs. 3–5, 9–12

Pleurophorus elegans Kirkby 1880, p. 586.

Carbonicola elegans Hind 1895, p. 81, pl. 20, figs. 12–15, 15a.

Type material. *C. elegans* was first described without figures from the No. 10 Limestone of Randerstone. Hind subsequently figured three complete specimens and a broken shell showing the hinge-plate, giving the locality as 'East of Pittenweem'. The evidence indicates that Hind was in error as to the locality of these specimens. Hind does not state that they are Kirkby's original material, but he acknowledges (1895, p. 82) the loan of material from Kirkby's collection. *C. elegans* occurs east of Pittenweem in a dwarf fauna from Bed 386 of Kirkby's Pittenweem–Anstruther section, but it seems improbable that the figured shells came from that locality. The writer has not found any specimens there as large as the figured shells, nor have any been observed in Kirkby's material in the Hancock Museum. The red limestone matrix of the figured shells is quite unlike pale grey ironstone of Bed 386, but is indistinguishable from the No. 10 Limestone, Randerstone. *C. elegans* is also found in Bed 649, at Billow Ness, 1 mile east of Pittenweem but much nearer to Anstruther. It is almost impossible to obtain a good specimen from this bed because of the nature of preservation of the fossils and it is unlikely that 'East of Pittenweem' refers to this locality. The writer is of the opinion that the figured shells are from the No. 10 Limestone, Randerstone, but that there is insufficient evidence to show whether they were Kirkby's original material.

EXPLANATION OF PLATE 25

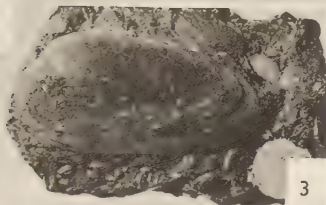
- Figs. 1–2. *Carbonicola antiqua* Hind. Calciferous Sandstone Series, red limestone, Kilminning, Crail, Fife, $\times 2$. 1, Lectotype, L.46889, complete shell. 2, Syntype, L.46890, right valve.
 Figs. 3–5. *Carbonicola elegans* (Kirkby). Calciferous Sandstone Series, Limestone 10, Randerstone, Fife. 3, L.47165, left valve, $\times 2$. 4, L.47163, right valve, $\times 2$. 5, L.47164, internal mould, $\times 2\frac{1}{2}$.
 Figs. 6–8. *C. antiqua*. Calciferous Sandstone Series, calcareous sandstone, Kilrenny Mill, Anstruther, Fife. 1001, internal mould, lateral, anterior, and dorsal views, $\times 2$.
 Figs. 9–12. *C. elegans*. Topotype material. 9–11, R.10.2, internal mould, anterior, lateral and dorsal views, $\times 2$. 12, In the collection of Dr. A. Wattison, internal mould showing muscle scars and pallial line, $\times 2\frac{1}{2}$.
 Figs. 13–14. *Anthraconaia? kirki* sp. nov. Calciferous Sandstone Series, mudstone, Kilrenny Mill, Anstruther, Fife. $\times 2\frac{1}{2}$. 13, holotype, S.13440, 14, paratype, S.13442.
 (Figs. 1–5 reproduced by permission of the British Museum (Nat. Hist.). Reg. nos.: prefix L denotes British Museum (Nat. Hist.); prefix S denotes Hunterian Museum, Glasgow; prefix R denotes University of St. Andrews collection. Remaining specimen in the author's collection.)



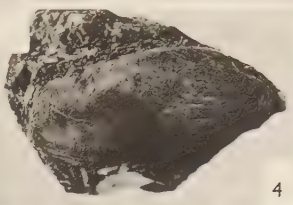
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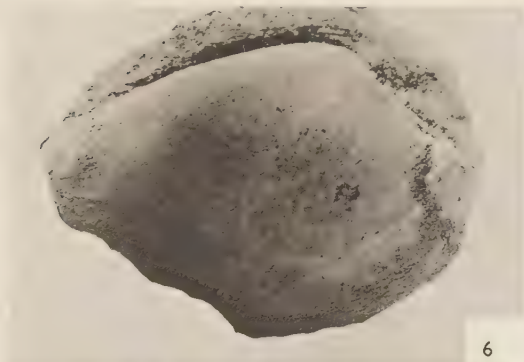
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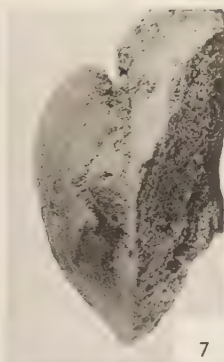
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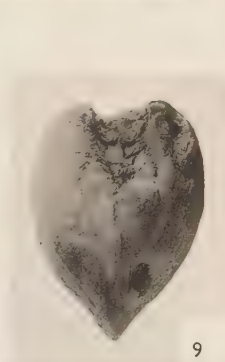
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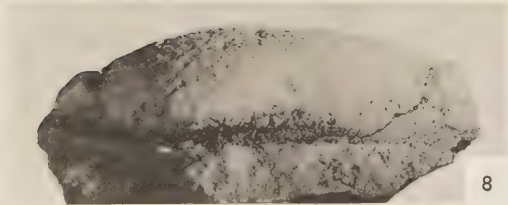
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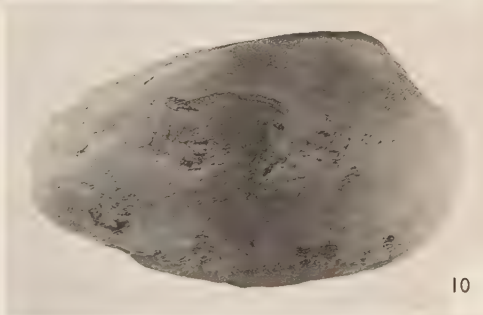
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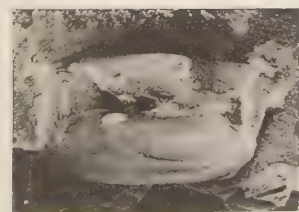
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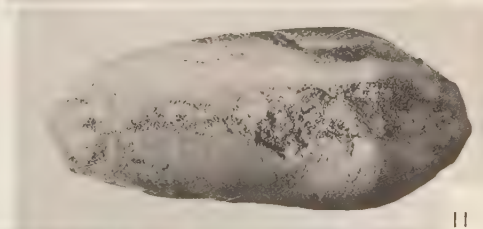
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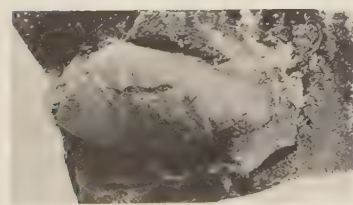
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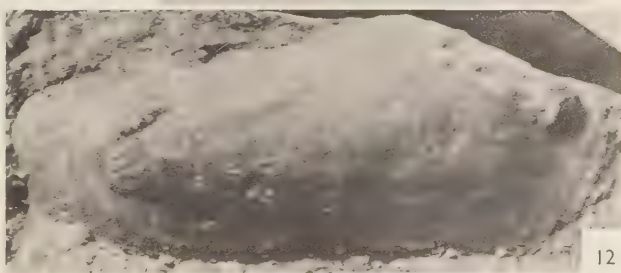
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11



14



12

Dimensions

	<i>L</i> (mm.)	<i>H</i> (mm.)	<i>A</i> (mm.)	<i>T</i> (mm.)
Pl. 25, fig. 3 (L.47165) (Hind, pl. 20, fig. 15)	17.6	8.5 (48.3%)	3.3 (18.7%)	est. 6.2 (35.2%)
Pl. 25, fig. 4 (L.47163) (Hind, pl. 20, fig. 13)	17.8	8.4 (47.2%)	3.7 (20.2%)	est. 6.0 (33.7%)

Description and discussion. Hind's specimens are larger than the mean for the topotype material from Randerstone. Shell ovate, elongate with H/L less than 50 per cent. Anterior end short, *c.* 20 per cent. of the length. Very fine, tilted growth lines. Moderately tumid. Lower border gently curved, posterior end rounded or obliquely truncated. Antero-umbonal slope concave. Slight carinate feature running downwards and backwards from umbo. Umbones low and directed towards the anterior. Edentulous. *C. antiqua* is thick shelled where it occurs in limestone and calcareous sandstone, but it is much thinner shelled where it is found in shale.

Comparison. *C. elegans* resembles *C. antiqua*, but the modal value of H/L is some 12 per cent. less. Growth lines are finer in *C. elegans* than in most variants of *C. antiqua*, and in no case have variants of the former with very coarse growth lines been observed. *C. elegans* and *C. antiqua* have not been found in the same bed; this mutual exclusion may indicate that they are biospecies. The variation of A/L in *C. antiqua* encompasses the variation of A/L in *C. elegans*, so that length of the anterior end is not a diagnostic character. The shape variation is more restricted in *C. elegans* and no variants with pronounced arching of the dorsal margin, nor variants which are skew ovals (due to the lowest part of the ventral margin being near the posterior end) such as are found in *C. antiqua*, have been observed.

Distribution. *C. elegans* has been recorded from Beds 386 and 649, separated by 1,200 feet of strata, of the Pittenweem–Anstruther shore, as well as from the No. 10 Limestone, Randerstone. It is clear from the correlation proposed by Kirkby (1880, p. 572), as modified by Kirk (1925, p. 369), that Bed 649 and the No. 10 Limestone must be at nearly the same horizon, but that they are not precise equivalents has been shown above.

Anthraconaia? kirki sp. nov.

Plate 25, figs. 13, 14

Holotype. Hunterian Museum, Glasgow, no. S.13440. *Paratype* no. S.13442.

Diagnosis. Small, elongate with a mean value for H/L approximately 40 per cent. for the four specimens measured. Anterior end short, not exceeding 20 per cent. of the length. Umbones low, anterior-umbonal slope concave. Hinge-line long and extending the greater part of the length of the shell. Posterior end rounded and slightly expanded. Greatest height of shell about one-third of the length from the posterior end. Ventral border gently curved. Growth lines fine, numerous, tilted. No distinct carina, but a swelling runs obliquely backwards and downwards from the umbo towards the posterior-inferior angle.

Dimensions

	<i>L</i> (mm.)	<i>H</i> (mm.)
Pl. 25, fig. 13 (S.13440), holotype .	9.6	3.3 (34.4%)
Pl. 25, fig. 14 (S.13442), paratype .	10.8	4.6 (43%)
S.13441	c. 12	6.0 (50%)
1139	14.9	5.7 (38%)

Only four measurable specimens have so far been obtained. Measurements of the length of the anterior end (not given here) are in the region of 1.5–2.5 mm., representing a value of 20 per cent., or less, for *A/L*.

Description. In two specimens both valves are present with the umbones in contact but they are agape. It is not possible to estimate tumidity as no specimens were obtained showing the original convexity. The angle β appears to be relatively low, just exceeding 100° , but the angle γ cannot be estimated from the limited material available. No evidence is available on the interior of the shell.

Comparison. *A.?* *kirki* is similar to the more elongate forms of *Anthraconaia* such as *A. williamsoni* or to *A. bellula* from the Millstone Grit. The following characters suggest the affinity of *A.?* *kirki* to *Anthraconaia*: the hinge-line and ventral margin are subparallel; the shell is expanded posteriorly; and it possesses an ill-defined carinal feature. Further, it forms a small percentage of a non-marine lamellibranch fauna. It seems preferable to refer this species to the genus *Anthraconaia* with a query, for Dr. J. Weir has pointed out to me that it is far removed in time from the typical *Anthraconaia* of the *adamsi-salteri-modiolaris* group, and that vital knowledge of the internal characters is lacking.

COMMUNITIES OF *CARBONICOLA*I. *Carbonicola antiqua*

1. *Kilminning.* *Carbonicola antiqua* is abundant in a 10-inch bed of red limestone at Kilminning, Fife, from which the syntypes were obtained. Specimens are poorly preserved and difficult to extract, but over 100 were examined and over ninety measured. The mean values for length, height, and length of anterior end of the shells from this collection are less than those for the collections from shale and sandstone at Kilrenny Mill.

	<i>L</i>	<i>H</i>	<i>A</i>	<i>d</i>	No. of specimens
Kilminning limestone . . .	20.6	12.4	3.9	8.6	91
Kilrenny Mill shale	22.0	13.8	5.1	9.7	62
Kilrenny Mill sandstone . .	23.1	13.6	4.7	..	13

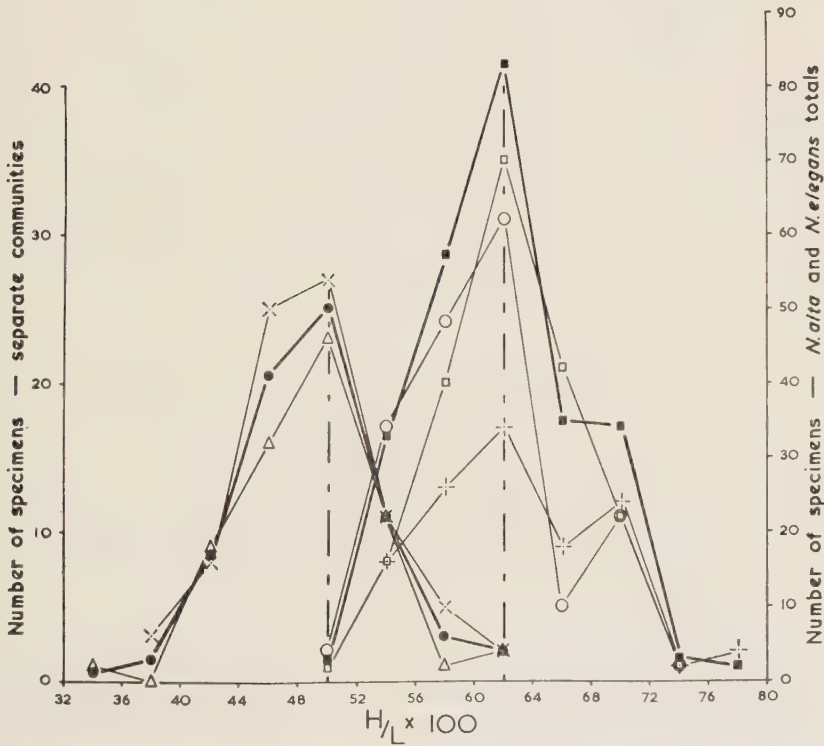
(Measurements in mm., only external measurements have been utilized.)

The abundance of shells in the Kilminning limestone and their eroded nature suggests that they have been sorted by wave or current action. The relatively high percentage of

small forms (less than 15 mm. in length) may be due to this sorting effect and the small range of variation in size confirms that this is not a life assemblage.

	% of specimens with L less than 15 mm.	% of specimens with L less than $\frac{2}{3}$ mean value	Range of value of L (mm.)
Kilminning Limestone . . .	17%	2% (less than 13.7 mm.)	13.4-28.2 (diff. 14.8)
Kilrenny Mill shale . . .	6%	6% (less than 14.5 mm.)	9.3-31.4 (diff. 22.1)
Kilrenny Mill sandstone . . .	1%	1% (less than 15.4 mm.)	14.5-25.9 (diff. 11.4)

- *Carbonicola antiqua* Kilminning 82 specimens
- +—+ *C. antiqua* Kilrenny Mill, shale 62 specimens
- *C. antiqua* Kilrenny Mill, sandstone 87 specimens
- *C. antiqua* all localities 231 specimens
- ×—× *C. elegans* No. 10 Limestone, Randerstone 81 specimens
- △—△ *C. elegans* dwarf fauna Bed 386, Pittenweem 63 specimens
- *C. elegans* both localities 144 specimens

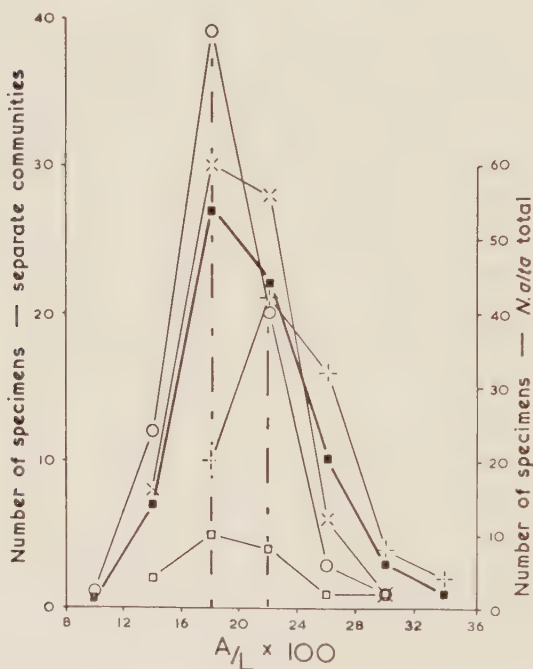


XT-FIG. 2. Graphs to show the ratio of length (L) to height (H) in collections of *Carbonicola antiqua* and *C. elegans* from east Fife.

The variation graph for H/L' (text-fig. 2) shows a modal value of 62 per cent. for the Kilminning shells, with a variation of 12 per cent. on either side of the mode. The other

collections show close agreement, both in mode and range of variation. The variation graph for A/L (text-fig. 3) shows that the Kilminning shells have a different modal value and a different range of variation from the Kilrenny Mill collections; the modal value for A/L is approximately 4 per cent. lower in the case of the Kilminning collection. Two factors might affect the proportions of the shells. The shells are rather small and if

○—○	<i>Carbonicola antiqua</i> Kilminning	76 specimens
+—+	<i>C. antiqua</i> Kilrenny Mill, shale	63 specimens
□—□	<i>C. antiqua</i> Kilrenny Mill, sandstone	13 specimens
■—■	<i>C. antiqua</i> all localities	152 specimens
×—×	<i>C. elegans</i> No.10 Lst., Randerstone	73 specimens

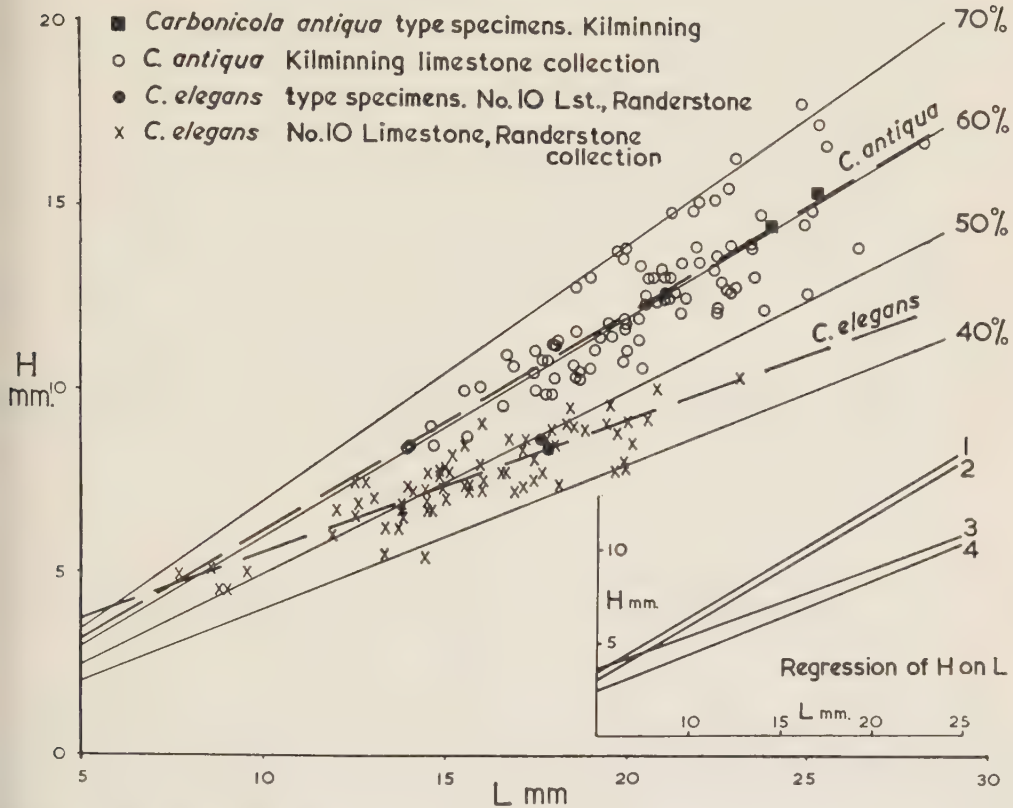


TEXT-FIG. 3. Graphs to show the ratio of length (L) to length of anterior end (A) in collections of *Carbonicola antiqua* and *C. elegans* from east Fife.

growth were allometric then the modal value of this collection would be low. A scatter diagram (text-fig. 5) does not reveal any tendency for length of anterior end to increase relatively with length and, calculating the regression of A on L, we find that the line would pass nearly through the intersection of the axes of the scatter diagram. The other factor affecting the proportions of the shells is the degree of crushing, related to the compaction of the sediment: this is noticeably less in the case of shells from the limestone than in shells from shale. The effects of crushing, if the shells are lying parallel to the bedding planes, as in this case, is to increase A/L; see Dix and Trueman (1931, p. 192) and Eagar (1947, p. 11). The second term, in a calculation of the slope of the

Regression line of A on L, is a measure of that slope: *C. antiqua*, Kilminning limestone $A = 0.25 + 0.176L$. *C. antiqua*, Kilrenny Mill shale $A = 0.45 + 0.256L$.

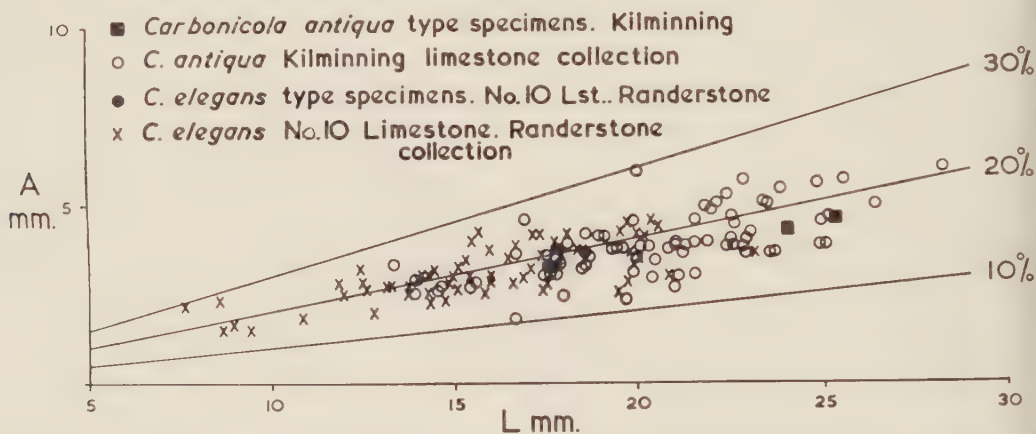
This seems to explain the discrepancy in the values of A/L in *C. antiqua*, and it seems unlikely that such a discrepancy may be attributed to evolutionary change or to a difference of habitat.



TEXT-FIG. 4. The relationship between length (L) and height (H) in *Carbonicola antiqua* and *C. elegans*. Inset: regression lines of H on L. 1 = *C. antiqua*, Kilrenny Mill shale collection, 2 = *C. antiqua*, Kilminning limestone collection, 3 = *C. elegans*, No. 10 Limestone, Randerstone collection, 4 = *C. elegans* dwarfs, Bed 386, Pittenweem collection.

In the collection from Kilminning T/L is high and variants with a bluntly rounded posterior end are relatively common. Variation in shape of shell is shown in text-fig. 6, which shows that some variants have a more pronounced dorsal arch, that some are new ovals, and that some have an obliquely truncated posterior. The first two kinds of variants have a relatively high value for H/L, but the presence of such variants is inadequately expressed by the simple H/L ratio. A fourth measurement, the distance from the anterior end to the point of maximum downward curvature of the lower border, noted by d, has been used (see Leitch 1940, p. 15). d/L is typically about 40 per cent., but ranges from 25 to 68 per cent.

2. *Kilrenny Mill shale*. *C. antiqua* is common in blue-grey shaly mudstone which almost immediately succeeds a highly fossiliferous calcareous sandstone. Many of the shells are excellently preserved, but they are less numerous than in the limestone of Kilminning and fewer measurable specimens were obtained. Individual shells here attain the greatest size. The shells show little evidence of sorting by wave action—although specimens often comprise single valves only—for there is here the greatest range in size and the greatest proportion of young (small, less than two-thirds the mean L) shells. This is, therefore, the most representative collection of *C. antiqua* and may approximate to a life assemblage. The assemblage includes about 8 per cent. of *Anthraconaia? kirki* and c. 2 per cent. of *Naiadites obesus* (R. Etheridge, jun.).



TEXT-FIG. 5. The relationship between length (L) and length of anterior end (A) in *Carbonicola antiqua* and *C. elegans*.

Variation in shape of shell is shown in text-fig. 7. It is apparent that variants with an obliquely truncated posterior end are more common than in the Kilminning collection, and a relatively large *pseudorobusta*-like variant (text-fig. 7L) is found in the Kilrenny Mill shale only. It is impossible to calculate the variation in shape of shell attributable to crushing effects and it is, therefore, questionable whether the shape variations, illustrated in text-figs. 6 and 7, represent true differences arising from adaption to environment or from evolutionary changes (Kirkby's view, that the shell beds of Kilminning and Kilrenny Mill could be correlated, has been discussed, and cannot be sustained).

3. *Kilrenny Mill sandstone*. In a calcareous sandstone of variable thickness (it is seen to thicken from 6 in. to 18 in. in a lateral distance of a few feet) *C. antiqua* is abundant. In most specimens the shell material has been dissolved away leaving excellent moulds, and, although these provide information on the internal character of *C. antiqua*, comparison with the other collections is difficult. In a few specimens the shell material is partially eroded and interior and exterior dimensions can be compared. It was observed that a correction made to the measurements of internal moulds, by adding 0.6 mm. to the length and height, was justifiable. The average shell thickness is of the order of 0.3 mm. and a comparison of the mean values of L, H, and H/L for the whole collection

with the correction applied) and the mean values obtained from the limited number of exteriors showed close similarity. No such correction was applied in the case of the anterior end, chiefly due to the difficulty of estimating the position of the umbo. The mean value of length, for this collection, is high but no very large shells have been found

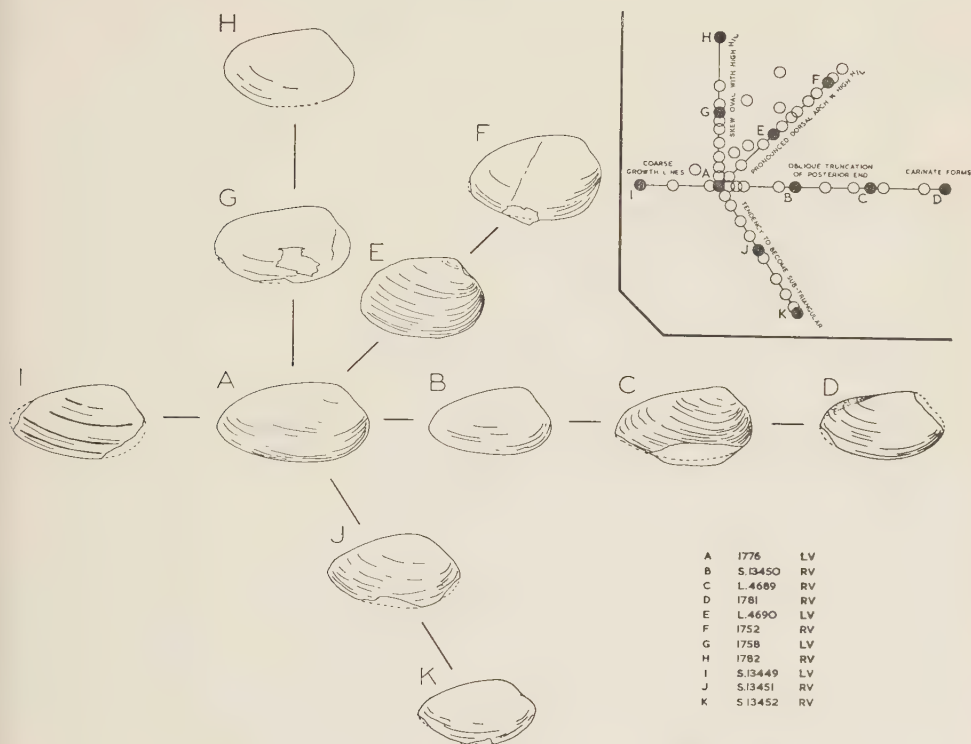


FIG. 6. Pictograph showing variation in shape of shell of *Carbonicola antiqua* from Kilminning, life. Inset shows distribution of variants relative to the figured specimens, which are represented by scattered black circles. For purposes of comparison all shells have been drawn as right valves. About two-thirds natural size. (Registered numbers with prefix L refer to Brit. Mus. (Nat. Hist.) specimens, with prefix S refer to Hunterian Mus., Glasgow specimens. Other specimens in author's collection.)

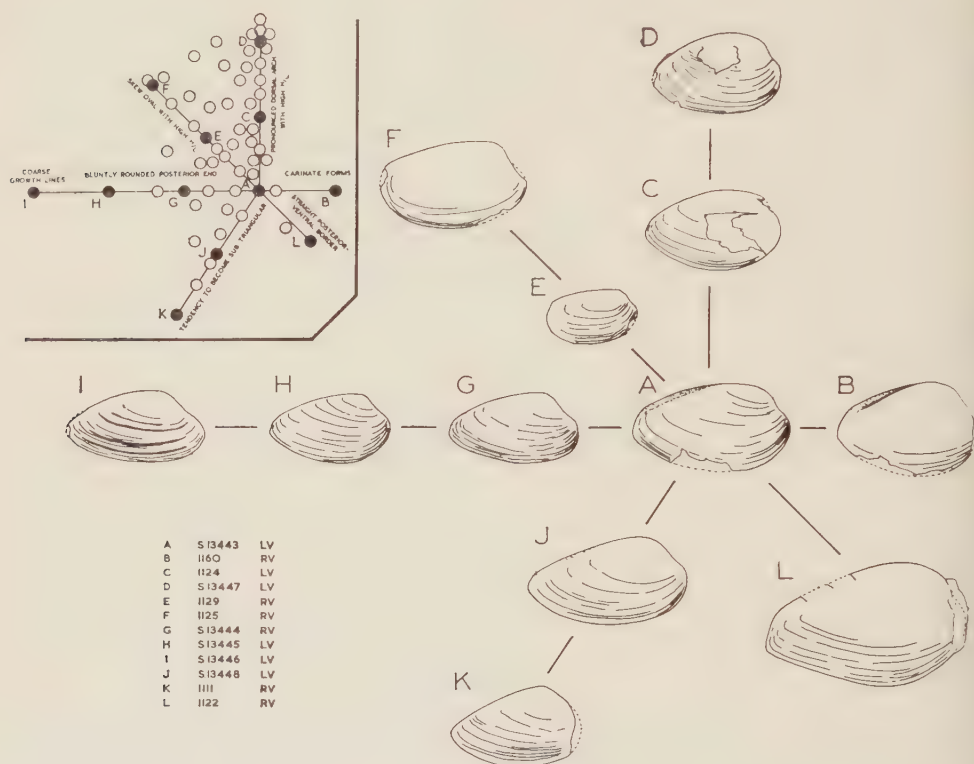
(see table above). Small shells are absent, providing evidence of sorting—as might be expected in a sediment with much detrital quartz.

Bed 586 of Kirkby's main section, Pittenweem-Anstruther shore. This exposure is covered by massive fallen blocks of sandstone. Only a few square inches of shale can be examined and, from these, three specimens of *C. antiqua* were obtained. Its presence is thus confirmed but comparison with collections from other localities is not possible.

Carbonicola elegans

Kirkby's No. 10 Limestone, 'Randerstone.' This is the only horizon from which *C. elegans* has been obtained in sufficient numbers to permit precise comparison with *C.*

antiqua. It is the probable horizon of Hind's specimens, and the horizon from which the species was first described by Kirkby. The collection shows a wide range of variation in the value of H/L, from c. 36 per cent. to 64 per cent., some variants having a value for H/L comparable with the modal value of the *C. antiqua* collections (text-fig. 2). The



TEXT-FIG. 7. Pictograph showing variation in shape of shell of *Carbonicola antiqua* from shale, Kilrenny Mill, Fife. Inset shows distribution of variants relative to the figured specimens, which are represented by lettered black circles. (For location of specimens see text-fig. 6.)

modal value of the *C. elegans* collection is 12 per cent. lower than that of the *C. antiqua* collections and, since no change in mode with horizon is known in either species, this appears to be a significant difference. Further, there is a tendency for H/L to decrease with increase in size of the individual in *C. elegans* (text-fig. 4); this is shown by calculating the regression of H on L. The regression line (text-fig. 4, inset, line 3) does not, if produced, pass through the origin of the graph. The difference between the slope of this line and the regression lines calculated for the Kilrenny Mill shale and Kilminning limestone collections of *C. antiqua* (lines 1, 2) are significant.

The modal value of A/L for this collection of *C. elegans*, 18 per cent., is close to that of the *C. antiqua* collections. The more reliable comparison can be made between the two limestone faunas, the Kilminning Limestone and the No. 10, Randerstone, for in

both the effects of crushing are at a minimum (text-figs. 4, 5). Calculation of the regression of A on L showed no statistically significant difference for the two species.

. *Bed 649 of Kirkby's main section, Pittenweem-Anstruther shore.* In this bed at Billow Ness, as Kirkby remarked (*in* Geikie 1902, p. 96), *C. elegans* occurs as a small percentage of a dominantly *Naiadites obesus* fauna. Usually the posterior-dorsal area of *N. obesus* is broken off, so that the shell bears a close resemblance to *C. elegans*. Because of this reservation it is difficult to estimate how commonly *C. elegans* occurs, but prolonged collecting has yielded a few well preserved shells which can be referred to that species without doubt.

. *Bed 386 of Kirkby's main section, Pittenweem-Anstruther shore.* A 3-inch bed of calcareous iron-rich siltstone includes dwarfed shells of *Carbonicola elegans*. The mean length of shell is less than 7 mm., less than half that of those from No. 10 Limestone, Randerstone. In measuring such small shells the operational error is liable to be high when expressed as a percentage of length or height. For this reason the same reliance cannot be placed on the H/L ratio although the modal value of 50 per cent. for this collection is comparable with that of the Randerstone shells and the regression lines (text-fig. 4 inset) are similar. The shells appear to resemble *C. elegans* in every way except size: they are, however, relatively thick shelled. It is difficult to establish whether the fauna is 'dwarfed' by adverse ecological conditions, or whether only small shells are present as a result of sorting by waves or currents. The former seems probable in view of the lithology (fine angular quartz grains are abundant and may have inhibited growth), and the range of variation in size of shell (L = 3 mm. to 11.5 mm.) does not confirm sorting effects. However, very young individuals (spat) are not present in the assemblage.

The following table shows the similarity of different collections of *C. antiqua*, differences due to relative amounts of crushing being reflected in regression equations of both

	<i>C. antiqua</i>			<i>C. elegans</i>	
	<i>Kilminning</i>	<i>K. Mill sh.</i>	<i>K. Mill sst.</i>	<i>No. 10 Lst.</i>	<i>Bed 386</i>
.	20.6 mm.	22.0 mm.	23.1 mm.	15.7 mm.	6.9 mm.
.	12.4 mm.	13.8 mm.	13.6 mm.	7.6 mm.	3.3 mm.
.	3.9 mm.	5.1 mm.	4.7 mm.	3.1 mm.	..
.	8.6 mm.	9.7 mm.	..	..	..
Mode H/L . . .	62%	62%	62%	50%	50%
Mode A/L . . .	18%	22%	18%	18%	..
Mode d/L . . .	42%	42%	..	..	..
Correlation:					
^r HL . . .	0.854	0.893	..	0.856	..
^r AL . . .	0.651	0.793	..	0.729	..
Regression:					
H =	0.25+0.593L	0.41+0.610L	..	1.82+0.368L	0.52+0.405L
A =	0.25+0.176L	0.45+0.256L	..	0.51+0.165L	..

on L and A on L. The greater difference between *C. antiqua* and *C. elegans* is indicated in the figures for H/L as well as the regressions.

CONDITIONS OF SEDIMENTATION

One of the features of *Carbonicola* from the Lower Carboniferous is its occurrence in rocks of widely differing lithology. It is found in calcareous, arenaceous, and argillaceous rocks. The question whether it could survive under such differing conditions of sedimentation arises. Further, if it lived in such a variety of environments, why should *C. antiqua* and *C. elegans* each occur at so few horizons, as far as is known, and be mutually exclusive of each other? In some cases, for example the No. 10 Limestone, the Kilminning limestone, and probably the Kilrenny Mill sandstone, the shells have been collected together by currents. The specimens are usually single valves and are probably not in their ecological stations. The occurrence of *C. antiqua* in the shaly mudstone of Kilrenny Mill probably provides the only reliable evidence of its ecology. The presence of large numbers of *C. antiqua* in the underlying sandstone is enigmatic, for this sediment comprises angular quartz grains cemented by calcite. The coarse texture of the rock, the variations in thickness of the bed, and the similarity in size of all the shells, together with the presence of macroscopic plant fragments, indicate turbulent conditions (Broadhurst 1959).

The habitat of *C. elegans* is even more difficult to assess. Only in the No. 10 Limestone of Randerstone is *C. elegans* abundant and here there is evidence of sorting. Petrologically, this rock could be classified as a microscopic limestone breccia. Apart from complete shells, the rock is made up largely of shell fragments of about 4 mm. diameter. It is surprising that *C. elegans* is not found in the shales immediately above the No. 10 Limestone in which *Naiadites obesus* is common, the more so since these two species occur together in Bed 649 at Billow Ness. Microscopic examination of the rock which yields the *C. elegans* dwarf fauna, Bed 386, reveals a matrix which includes 40 per cent of angular quartz grains (0.1 mm. in diameter). This silt may have inhibited the growth of *C. elegans*.

C. antiqua and *C. elegans* are found in beds which occur in a succession which is not dominantly marine, but which includes shales and limestones with varied marine faunas. The absence of contemporaneous marine forms (but see below) from the *C. antiqua* and *C. elegans* shell beds is an indication of their non-marine habitat. Both species are found in association with *Naiadites obesus* which, elsewhere, is found in close proximity to marine forms. The only other faunal associations of these species of *Carbonicola* are with *Spirorbis* (cf. the association of *Spirorbis* with non-marine shells noted by Etheridge (1800, p. 217); see also Trueman (1942) and with ostracods. Kirkby (1880, p. 577) records the presence of numbers of *Littorina scotoburdigalensis* with *Carbonicola elegans*. Hind (1895, p. 82) notes that Etheridge believed this gastropod to be 'nearer to *Paludina*' (= *Viviparis*, a fresh-water form). Unfortunately the author has not found any specimens of it. Kirkby (in Geikie 1902) records only three species of ostracod in association with *C. elegans*, namely *Cytherella attenuata*, *C. extuberata*, and *Cythere superba*. Latham (1932) showed that these are among the commonest forms in the Calcareous Sandstone Series, are of long range, and occur in varied faunal associations, frequently with *Naiadites obesus* but also with *Schizodus* and other marine lamellibranchs. The known faunal associations of the two Calcareous Sandstone Series species of *Carbonicola* are summarized:

<i>Carbonicola antiqua</i>	<i>Carbonicola elegans</i>
<i>Naiadites obesus</i>	<i>Naiadites obesus</i>
<i>Spirorbis</i> sp.	<i>Spirorbis</i> sp.
<i>Anthraconaia?</i> <i>kirki</i>	? <i>Littorina scotoburdigalensis</i>
<i>Cytherella</i> sp.	<i>Cytherella attenuata</i>
Fish teeth	<i>Cytherella extuberata</i>
	<i>Cythere superba</i>
	Fish teeth and spines

The presence of macroscopic drifted plant fragments, occurring on the same bedding planes as the shells, indicates the proximity of land. Little can be said to account for the mutual exclusion of *C. antiqua* and *C. elegans*; the only observed difference in the matrices was the relative abundance of iron in the shell beds including *C. elegans*. The presence of one species rather than the other may well be related to salinity or temperature, environmental characters which are not reflected in the lithology.

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AMMONOIDS AND TRILOBITES FROM THE UPPER DEVONIAN AND LOWEST CARBONIFEROUS OF THE LAUNCESTON AREA OF CORNWALL

by E. B. SELWOOD

ABSTRACT. An ascending sequence of strata, comprising the Petherwin Beds, the Stourscombe Beds, and the Yeolmbridge Beds, is noted at the Devonian–Carboniferous boundary. The ammonoid and trilobite fauna of these beds is described.

The genus *Kenseyoceras* and the contained subgenus *K. (Mayneoceras)* are proposed, and *Epiwocklumeria* is defined. The following species are redescribed or proposed:

Petherwin Beds (*Platyclymenia* and *Clymenia* Zones): *P. (Platyclymenia) valida* (Phillips), *P. (Platyclymenia) pattisoni* (M'Coy), *Costaclymenia muensteri* (Ansted). Stourscombe Beds (*Wocklumeria* Zone); *Wocklumeria pharoides* (Rh. Richter), *Epiwocklumeria dunhevedensis* sp. nov., *Kosmoclymenia pattisoni* sp. nov., *Cymaclymenia constricta* sp. nov., *C. constricta* var. *globosa* nov., *Parawocklumeria laevigata* sp. nov., *P. laevigata* var. *besa* nov., *Parawocklumeria* sp., *K. (Kenseyoceras) rostrata* gen. and sp. nov., *K. (Mayneoceras) sinuconstricta* (n. gen. and sp. nov., *Discoclymenia cornwallensis* sp. nov., *D. aff. cornwallensis* sp. nov. Yeolmbridge Beds (*Gattendorfia* Zone): *C. (Macrobole) drewerensis* Rud. & E. Richter sens nov., *C. (Macrobole) sp.*

For many years it was considered that rocks of highest Devonian and lowest Carboniferous age were unrepresented on the southern limb of the great Culm synclorium of Devon and Cornwall. Recently ammonoids and trilobites, the subject of this paper, have been collected from a series of beds hitherto undifferentiated in the Launceston district of Cornwall; these fossils show that a complete succession of beds is represented between the Devonian and Carboniferous systems at Launceston.

The Petherwin Beds, the Stourscombe Beds, and Yeolmbridge Beds constitute the ascending sequence of strata at the Devonian–Carboniferous boundary. Faunas from the Petherwin Beds have been known since the area was first surveyed by the Geological Survey (de la Beche 1839). The Stourscombe Beds and the Yeolmbridge Beds are newly identified stratigraphical units recognized within the area mapped as Lower Culm by the Geological Survey (Tavistock and Launceston Sheet—No. 337).

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Specimens which have been described and figured in the palaeontological part of this paper are placed in museums which have been abbreviated in the descriptions as follows: GSM, Geological Survey Museum, London. BM, British Museum (Nat. Hist.), London. SMC, Sedgwick Museum, Cambridge. BU, Geology Museum, University of Bristol. PMC, Penzance Museum, Cornwall.

All localities mentioned in the text are to be found on the Ordnance Survey One inch Sheet No. 186, and are referred to by their O.S. National Grid Reference.

The terminology used in the descriptions of the ammonoids is similar to that employed in the *Treatise on Invertebrate Paleontology (Part L. Mollusca)*; foreign specimens, included in tables for comparative purposes, are referred to by the date of the

paper from which the information was taken. Abbreviations are to be interpreted as follows: W. T.—whorl thickness, W. H.—whorl height, D.—diameter, U.—umbilicus. The trilobite terminology is that of Goldring (1955).

STRATIGRAPHY

The Petherwin Beds

The Geological Survey (Reid *et al.* 1911) applied the name Petherwin Beds to a thick succession of slates containing thin calcareous bands with brachiopods, and also to thicker limestones with abundant ammonoids which are associated with the slates. The stratigraphical relationships of these two lithologies cannot be determined in the field. However, it appears highly probable that the ammonoid-bearing limestones, which represent a very different sedimentary facies from the main bulk of the slates, are not interbedded with them, but constitute an underlying group of strata. The brachiopod slates are here referred to the Upper Petherwin Beds and the ammonoid bearing limestones and associated strata, which include a sandstone, to the Lower Petherwin Beds.

The Lower Petherwin Beds. Only two exposures yield fossils of the Lower Petherwin Beds at the present time. The more complete section is at the locality described (Reid *et al.* 1911) as the Gatepost Quarry (SX 326 821). The fauna, which is largely confined to a rottenstone horizon, includes:

- | | |
|---|---|
| <i>Gonioclymenia</i> (<i>Kalloclymenia</i>) <i>biimpressa</i> (von Buch 1839)—BU 12876. | <i>Cymaclymenia striata</i> (Münster 1832)—BU 12872, 12873. |
| <i>Clymenia hoevelensis</i> (Wedekind 1914)—BU 12864. | <i>C. camerata</i> Schindewolf 1923—BU 12874, 12875. |
| <i>Kosmoclymenia undulata</i> (Münster 1832)—BU 12868–70. | <i>Imitoceras</i> cf. <i>lineare</i> (Münster 1832)—BU 12878. |
| <i>K. bisulcata</i> (Münster 1840)—BU 12867. | <i>Phacops</i> (<i>Phacops</i>) <i>granulatus</i> (Münster 1840)—BU 12917, 12918. |
| <i>K. sedgwicki</i> (Münster 1840)—BU 12871. | <i>P. (Phacops) accipitrinus</i> (Phillips 1841)—BU 12926, 12927. |

The second locality is at a neighbouring road section, by Oldwit Farm (SX 319 819), where the following have been identified:

- | | |
|--|--------------------------|
| <i>Gonioclymenia</i> (<i>Kalloclymenia</i>) <i>sp.</i> | <i>Kosmoclymenia sp.</i> |
| <i>Clymenia hoevelensis</i> (Wedekind 1914)—BU 12865, 12866. | <i>Cymaclymenia sp.</i> |

The ammonoids obtained from these two localities show that the fauna of the Lower Petherwin Beds is closely comparable to that of the lower (*Clymenia hoevelensis*) sub-zone of the German *Clymenia* Zone.

An examination of the available specimens from the Launceston district in the Geological Survey Museum, the British Museum (Nat. Hist.), the Sedgwick Museum, and the Museum at Penzance reveals that a number of species formerly collected from the beds is not present in the fauna from the two localities mentioned above. The species in question are characteristic of the *Platyclymenia* Zone of the continental succession. It thus appears that the strata referable to this zone were formerly exposed in the district. Many of the specimens in the old collections are not properly localized, but most of them certainly come from the old limestone quarry at Landlake (SX 328 823) now com-

pletely filled with refuse. Enough specimens are clearly labelled as coming from this quarry to make it certain that the *Platyclymenia* Zone was exposed there. In addition, specimens of the same species as those occurring in the Gatepost Quarry have also been recorded from this quarry; it is thus evident that the lower *Clymenia* Zone was also once exposed. The fauna, with revised identifications, of the Landlake Limestone Quarry is as follows:

- Costaclymenia muensteri* (Ansted 1838)—SMC H4010.
Gonioclymenia (*Kalloclymenia*) *biimpressa* (von Buch 1839)—GSM 7083.
Platyclymenia (*Platyclymenia*) *walcotti* Wedekind 1914—GSM 57322.
Platyclymenia (*Platyclymenia*) *richteri* Wedekind 1914—GSM 57323, 57327.
Platyclymenia (*Platyclymenia*) *annulata* (Münster 1832)—?GSM 57328.
Platyclymenia (*Platyclymenia*) *valida* (Phillips 1841)—GSM 7176.
Platyclymenia (*Platyclymenia*) *bicostata* Wedekind 1914—SMC H992.
Platyclymenia (*Platyclymenia*) *pattisoni* (M'Coy 1851)—SMC H990.
Clymenia hoevelensis (Wedekind 1914)—GSM 57314, 57315, 57324; SMC H989, H4012.
Kosmoclymenia undulata (Münster 1832)—GSM 57317, 57318, 7176; BM 37955; SMC H4011, H4013, H1488; PMC 152.
K. bisulcata (Münster 1840)—SMC H988.
K. sedgwicki (Münster 1840)—GSM 57325, 57326; SMC H1487; BM C51014.
K. linearis (Münster 1832)—?GSM 57316.
Cyrtoclymenia plicata (Münster 1839)—GSM 7174, ?7172.
C. angustiseptata (Münster 1832)—BM 37827.
Imitoceras cf. *disciforme* Schindewolf 1923—GSM 57300.
I. cf. quadripartitum (Münster 1839)—GSM 57303.
Sporadoceras rotundum Wedekind 1908—GSM 57301.
Phacops (*Phacops*) *granulatus* (Münster 1840)—PMC 113.
Cyrtosymbole (?*Waribole*) *dunhevedensis* (Thomas 1909).

The Upper Petherwin Beds. Ammonoids and trilobites are particularly rare in the Upper Petherwin Beds. A single distorted specimen of the genus *Kosmoclymenia*, together with a trilobite cranidium referable to the subgenus *C.* (*Waribole*), has been discovered in the brachiopod slates of the Lower Landlake Slate Quarry (SX 328 824).

The Stourscombe Beds

The name Stourscombe Beds has been used for a group of nodular and thin-bedded limestones and slates which have yielded a rich fauna of ammonoids and trilobites. The ammonoid fauna has largely been collected from the nodular development of the Stourscombe Beds seen in two disused quarries near Stourscombe (SX 344 839). In the westerly quarry it has been possible to divide the beds into two faunal divisions; an upper division characterized by the genus *Wocklumeria* and a lower division in which *Parawocklumeria* is abundant and *Wocklumeria* absent. This faunal division may be compared closely to the subzone of *P. paradoxa* (Wedekind) which forms the upper part of the *Wocklumeria* Zone in Germany. The fauna from Stourscombe includes:

- Gonioclymenia* (*Kalloclymenia*) *frechi* Lange 1929—GSM 87075; BU 12802, 12803.
G. (Kalloclymenia) wocklumensis Lange 1929—GSM 87076, 87077; BU 12799–801.
Wocklumeria sphaeroides (Rh. Richter 1848)—GSM 87033–7; BU 12824–8.
Epiwocklumeria dunhevedensis sp. nov.—GSM 87038.
Postglatziella carinata Schindewolf 1937—GSM 87039, 87040; BU 12815, 12816.
Kosmoclymenia undulata (Münster 1832)—GSM 87097; BU 12808, 12809.
K. bisulcata (Münster 1840)—GSM 87041; BU 12810, 12811.
K. linearis (Münster 1832)—GSM 87042; BU 12806, 12807.

- K. wocklumeri* (Wedekind 1914)—GSM 87078; BU 12805.
 **K. serpentina* (Münster 1832)—BU 12804.
 **K. pattisoni* sp. nov.—GSM 87043.
Cyrtoclymenia plicata (Münster 1839)—GSM 87080.
C. angustiseptata (Münster 1832)—BU 12813, 12814.
 **C. tetragona* Schmidt 1924—GSM 87044; BU 12812.
Cymaclymenia striata (Münster 1832)—BU 12836.
 **C. striata* var. nov.—GSM 87045, 87046.
 **C. cordata* Wedekind 1914—GSM 87047.
C. camerata Schindewolf 1923—GSM 87048; BU 12843, 12853.
C. constricta sp. nov.—GSM 87049, 87050; BU 12837, 12839–42.
C. constricta sp. nov. var. A nov.—GSM 87052.
 **C. constricta* sp. nov. var. *globosa* nov.—GSM 87051.
 **Parawocklumeria laevigata* sp. nov.—GSM 87053–6; BU 12829–34.
 **P. laevigata* sp. nov. var. *obesa* nov.—GSM 87088.
 **Parawocklumeria* sp.—GSM 87057.
Kensyoceras (*Kensyoceras*) *rostrata* subgen. et sp. nov.—GSM 87058–63; BU 12844–7.
K. (Mayneoceras) sinuconstricta subgen. et sp. nov. GSM 87069; BU 12835.
K. (Mayneoceras) nucleus (Schmidt 1924)—GSM 87064–8; BU 12848–9.
Imitoceras lineare (Münster 1832)—GSM 87083; BU 12819, 12820.
I. substriatum (Münster 1840)—GSM 87084; BU 12882.
I. intermedium Schindewolf 1923—GSM 87085; BU 12821.
I. varicosum Schindewolf 1923—GSM 87086.
 **I. subbilobatum* (Münster 1839)—GSM 87087.
 **Discoclymenia cucullata* (von Buch 1839)—GSM 87070.
 **D. cornwallensis* sp. nov.—GSM 87071, 87072.
 **D. aff. cornwallensis* sp. nov.—GSM 87073.
 **Sporadoceras orbiculare* (Münster 1832)—BU 12817, 12818.
 **S. orbiculare* var.—GSM 87074.
Phacops (*Phacops*) *granulatus* (Münster 1840)—BU 12920, 12921.
P. (Phacops) accipitrinus accipitrinus (Phillips 1841)—BU 12928.
P. (Phacops) wedekindi Rud. & E. Richter 1926—BU 12930–2.
P. (Phacops) ensae Rud. & E. Richter 1926—BU 12935–8.
P. (Cryphops?) wocklumeriae Rud. & E. Richter 1926—BU 12943–4.
 **P. (Dianops) sp.*—GSM 87091.
 **Chaunoproetus aff. carnicus* (Rud. Richter 1913)—GSM 87092.
 * Lower faunal division only.
 † Upper faunal division only.

A few ammonoids have been collected from Overwood Farm (SX 303 873). At this locality there are relatively few siliceous nodules, and the majority of these are unfossiliferous. The slates, on the other hand, have yielded a large number of trilobites. The fauna from this locality includes:

- G. (Kalloclymenia) sp.*
Wocklumeria sp.
Cyrtoclymenia angustiseptata (Münster 1832)—GSM 87081.
Parawocklumeria sp.
Phacops (*Phacops*) *granulatus* (Münster 1840)—BU 12923–5.
P. (Phacops) accipitrinus accipitrinus (Phillips 1841)—BU 12929; PMC 100 (labelled 'Near Yeolmbridge').
P. (Cryphops?) ensae Rud. & E. Richter 1926—BU 12940–2.
Cyrtosymbole (Waribole) cf. warsteinensis Rud. & E. Richter 1926—BU 12945–7.
C. (Waribole) aff. conifera Rud. & E. Richter 1926—GSM 87093; BU 12951.
C. (Waribole) aff. italica (Gortani 1907)—GSM 87094–5; BU 12956, 12957.
C. (Macroboule?) aff. bergica Rud. Richter 1913—GSM 87096; BU 12962, 12963.
C. cf. nepia Rud. & E. Richter 1926—BU 12958–60.

Similar trilobite-bearing slates occur at three localities in the Devonian inlier at Lifton; Heale Farm (SX 362 862), Smallacombe Farm (SX 375 860), and Coombe Farm (SX 386 858).

The slates with thin cherts, which form the more extensive development of the Stourcombe Beds, are generally unfossiliferous. Formerly these beds were included in the

lower Carboniferous, but the discovery of a single specimen (GSM 87082) of *Parawocklumeria distorta* (Tietze 1870) from a locality north-north-west of Oldtree Lodge (SX 306 46) and other ammonoids from widely separated localities now enables these slates to be correlated with the upper part of the *Wocklumeria* Zone.

The Yeolmbridge Beds

The name Yeolmbridge Beds has been applied to a series of slates, sandstones, and siltstones which conformably succeed the Stourscombe Beds.

The fauna from these beds is largely restricted to two localities; at Penfoot (SX 302 833) and Yeolmbridge (SX 322 875). At Penfoot the bulk of the fauna has been obtained from nodular limestone and includes:

- | | |
|---|--|
| <i>Gattendorfia subinvoluta</i> (Münster 1839)—BU 12886–90. | 12895. |
| <i>G. crassa</i> Schmidt 1924—BU 12882–3. | <i>I. cf. substriatum</i> (Münster 1840)—BU 12896. |
| <i>G. tenuis</i> Schindewolf 1952—BU 12885. | <i>C. (Macrobole) drewerensis</i> Rud. & E. Richter 1951—BU 12904–8. |
| <i>G. occlusa</i> Librovice 1940—BU 12884, 12915. | <i>C. (Macrobole) duodecimae</i> Rud. & E. Richter 1951—BU 12911, 12912. |
| <i>Ammonitoceras lineare</i> (Münster 1832)—BU 12893. | |
| <i>cf. intermedium</i> Schindewolf 1923—BU 12894, | |

At Yeolmbridge the fauna has been obtained from two exposures in the disused Yeolmbridge Slate Quarry; one consisting of a fresh limestone on the north side of the quarry, and the other of decalcified lentils occurring in a sandy slate on the south side of the quarry. The fauna includes:

- | | |
|---|---|
| <i>Gattendorfia</i> sp.—BU 12892. | <i>C. (Macrobole) duodecimae</i> Rud. & E. Richter 1951—GSM 87100; BU 12913, 12914. |
| <i>Ammonitoceras</i> sp. | <i>C. (Macrobole) aff. blax</i> Rud. & E. Richter 1951—GSM 87101; BU 12910. |
| <i>Cyrtosymbolites (Macrobole) drewerensis</i> Rud. & E. Richter 1951—GSM 87098, 87099; BU 12901–3. | <i>C. (Macrobole) sp.</i> —GSM 87097; BU 12909. |

The fauna obtained from these localities in the Yeolmbridge Beds is very similar to that obtained from the *Gattendorfia* Zone of the Continent.

SYSTEMATIC DESCRIPTIONS

Ammonoids

Family GONIOCLYMENIIDAE Hyatt 1884
Genus COSTACLYMENIA Schindewolf 1920
Costaclymenia muensteri (Ansted 1838)

Plate 26, fig. 1

- 1838 *Endosiphonites münsteri* Ansted, p. 419, pl. 8, fig. 1.
1852 *Clymenia muensteri* M'Coy, p. 402, pl. 2A, fig. 12.
1950 *Costaclymenia binodosa* G. & H. Termier, p. 77, pl. 160, figs. 28–30.

Paratype (by monotypy). SMC H4010. Pl. 26, fig. 1.

Type locality. Landlake Limestone Quarry, nr. Launceston.

Horizon. Lower Petherwin Beds.

Remarks. Gümbel (1863) states that *C. muensteri* is identical to *Clymenia binodosa* which was figured by Münster in 1839 (pl. 2, figs. 3a–c). On this contention Ansted's name

should have had priority, but it was not used because Münster's species was allegedly conspecific with *Goniatites binodosus* Münster 1832 (pl. 6, figs. 5a, b). However, the two specimens figured by Münster are not obviously conspecific, and since *C. muensteri* is quite distinct from Münster's earlier figures Ansted's species is still valid.

Only a single specimen has been recorded, and although this specimen closely resembles *C. binodosa* (Münster 1839) it is not considered to be identical to it, for the ribs and tubercles are more numerous and less prominent. In addition the whorl flanks in *C. muensteri* converge slightly towards the venter, whereas the whorl cross-section of *C. binodosa* is rectangular.

The whorl cross-section and the rather weak ornament make the specimens figured by G. & H. Termier (1950) closer to *C. muensteri* than to *C. binodosus*.

Mr. A. G. Brighton has drawn the author's attention to a manuscript note with the specimen which reads: 'It appears to have been subsequently to the drawing of Ansted's figure broken, and in that state was refigured by M'Coy. . . . Since then the greater part of the missing piece has been restored.'

Measurements of holotype (in mm.). D. 97, W.H. 36, W.T. 18, U. 41.

Genus GONIOCLYMENIA Hyatt 1884

Subgenus GONIOCLYMENIA (KALLOCLYMENIA) Wedekind 1914

Remarks. The genus *Kalloclymenia* was erected by Wedekind in 1914, and distinguished from *Gonioclymenia* with which its species had previously been included by the following characters: (a) the absence of a spiral groove on the venter, (b) the nature of the ribs, and (c) the lower rectangular whorl cross-section. The suture-line is, by diagnosis, indistinguishable from that of *Gonioclymenia*. Lange (1929) observed that only the first criterion is valid for generic diagnostic purposes and suggested that the name *Kalloclymenia* be reduced to subgeneric status.

In the *Treatise on Invertebrate Paleontology* (1957) the generic status of *Kalloclymenia* is reaffirmed with a note that the ventral sinus and the low rectangular whorl cross-section are diagnostic. The author does not agree with the latter contention, for *G. (K.) wocklumensis* Lange 1929 in particular has a whorl section in which the whorl height is considerably in excess of the whorl thickness. It is therefore proposed to continue the usage of Lange, for the important stratigraphical position which has been ascribed to *Kalloclymenia* on the Continent, which might conceivably warrant generic status, is not valid in Cornwall.

On the Continent the incoming of *Kalloclymenia* has proved a useful datum to mark the lower limit of the *Wocklumeria* Zone. In Cornwall, however, *Kalloclymenia* occurs earlier, for it has been found associated with the index fossil of the lower *Clymenia* Zone in the Petherwin Beds. It thus appears that the lower limit of the *Wocklumeria* Zone needs redefinition. This problem will be discussed in a later paper on the stratigraphy of the area.

The reduction of *Kalloclymenia* to a subgenus of *Gonioclymenia* raises the question of the status of *Otoclymenia* Schindewolf 1923, for this genus was reduced (Schindewolf 1937) to a subgenus of *Kalloclymenia*. The distinctive ornament of parabolic ribs and nodes undoubtedly means that it should be distinguished from *Kalloclymenia*; it is suggested that *Otoclymenia* be referred to a new subgenus of *Gonioclymenia*.

Gonioclymenia (Kalloclymenia) biimpresa (von Buch 1839)

Plate 26, fig. 2

1841 *Goniatites insignis* Phillips, p. 119, pl. 49, fig. 228.1929 *Gonioclymenia (Kalloclymenia) biimpresa* Lange, p. 80, pl. 2, fig. 20, text-figs. 16, 17.1950 *Gonioclymenia insignis* G. & H. Termier, p. 77, pl. 160, figs. 20–22.

Remarks. *Goniatites insignis* was referred by Gümbel (1863) to *Gonioclymenia subarmata* Münster), but the specimen figured by Phillips lacks the characteristic, rather noded ornament of Münster's species (1832, pl. 6, fig. 2). The ornament is much closer to that of *G. (Kalloclymenia) biimpresa* (von Buch), the holotype of which was refigured by Lange (1929). It does seem, however, that the ornament persists in the British specimens on to more mature whorls than on the holotype.

Measurements of figured specimen (GSM 7083) (in mm.). D. 61, W.H. 15.5, U. 34.

Gonioclymenia (Kalloclymenia) frechi Lange 19291929 *Gonioclymenia (Kalloclymenia) frechi* Lange, p. 81.

Remarks. The specimens occurring in Cornwall are very close to the described species but show a relatively greater whorl height.

Gonioclymenia (Kalloclymenia) wocklumensis Lange 19291929 *Gonioclymenia (Kalloclymenia) wocklumensis* Lange, p. 79, pl. 2, figs. 18, 18a, text-figs. 14, 15.

Remarks. In the Cornish specimens the whorl height is relatively greater, and the convergence of the flattened flanks at the venter is less than that indicated in Lange's original description. It has been observed that the mature suture line does not develop until approximately the fifth or sixth whorl; i.e. a diameter of some 15 mm. The adventitious lobe does not make its appearance until the fourth whorl. The whorl cross-section in the young stages is much squarer than that exhibited in the mature form.

Family WOCKLUMERIIDAE Schindewolf 1937

Genus WOCKLUMERIA Wedekind 1918

Wocklumeria sphaeroides (Rh. Richter 1848)

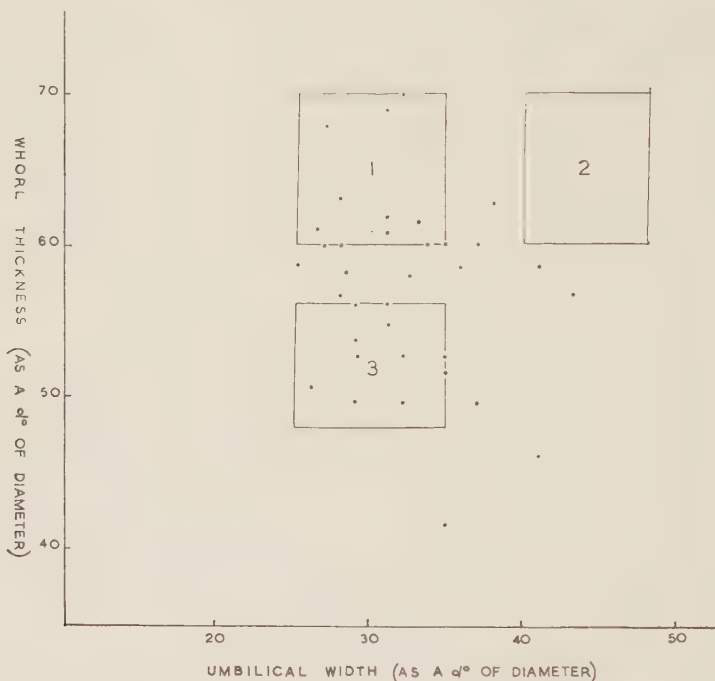
Plate 26, figs. 3–5; text-fig. 1

1937 *Wocklumeria sphaeroides* Schindewolf, p. 69, pl. 1, figs. 12–15; pl. 2, figs. 1–3, text-fig. 12 (with previous synonymy).1937 *Wocklumeria plana* Schindewolf, p. 70, pl. 2, figs. 4–6.1937 *Wocklumeria aperta* Schindewolf, p. 71, pl. 2, figs. 7–9, text-fig. 14.1954 *Wocklumeria sphaeroides* Pfeiffer, p. 58, pl. 8, figs. 5, 6.1954 *Wocklumeria plana* Pfeiffer, p. 58, pl. 8, fig. 7.

Remarks. The genus *Wocklumeria*, monospecific when erected by Wedekind (1918), was investigated by Schindewolf (1937) who, after a study of many specimens, recognized two additional species *W. plana* and *W. aperta*, closely related to the genotype.

A study of a number of specimens from Cornwall has revealed a much greater variability than was noticed by Schindewolf in his material. A number of gradational forms have been found between *W. plana* and *W. sphaeroides*, and between *W. aperta* and *W.*

sphaeroides. The scatter diagram (text-fig. 1) shows that there is a complete gradation existing between the extreme globose and extreme discoidal forms. The suture-lines of the two species recognized by Schindewolf in this range are, by diagnosis, identical; thus the remaining distinguishing feature is the height of the aperture. Since '*sphaeroides*' forms have been seen with '*plana*' apertures and vice versa there appears no reason to separate the two.



TEXT-FIG. 1. Scatter diagram of specimens of *Woeklumeria* from the Stourscombe Beds. The limits of species defined by Schindewolf are indicated thus: (1) *W. sphaeroides*, (2) *W. aperta*, (3) *W. plana*.

In both German and British specimens there is a preponderance of specimens within the limits formerly defining *W. sphaeroides* and *W. plana*. No Cornish specimen falls within the limits of *W. aperta* as defined by Schindewolf, though several specimens are very close to it. Since Schindewolf defined *W. aperta* on only six specimens there is probably no significance in this fact and nothing to indicate an interruption in the continuous variation of *W. sphaeroides*.

In the light of this evidence, there appears little basis for the division of the range of forms of *W. sphaeroides*; *W. plana* and *W. aperta* are consequently here considered to be synonyms of Richter's species. It has thus become necessary to redefine *W. sphaeroides* in more general terms.

Diagnosis. *Woeklumeria* with discoidal to globose shell, moderately wide umbilicus and low aperture. Young forms triangular in outline impressed by three deep constrictions; adult stage rounded, normally lacking constrictions. Ventral lobe deep, pointed, first lateral saddle rounded passing into a moderately wide and pointed first lateral lobe; this

be is as deep or deeper than the ventral lobe. Second lateral saddle rounded, umbilical lobe broad, divided at the umbilical seam by a strong saddle; prongs of umbilical lobe pointed. Dorsal lobe pointed, with almost parallel sides. First and second dorso-lateral saddles rounded, separated by pointed dorso-lateral lobe.

Description. Shell discoidal to globose, involute, greatest thickness at the umbilicus. Five to six whorls, involution considerable, umbilicus moderately large to small, deep; revealing the triangular shape of the earlier whorls. Laterally whorls slightly to moderately compressed, strongly rounded ventrally, flanks deeply impressed by the preceding whorl, aperture small. Body chamber one whorl, anterior portion deviating from the normal whorl spiral, thus considerably increasing the size of the umbilicus at this point. Aperture marked posteriorly by a constriction. Suture-line, see Schindewolf (1937, text-figs. 12a, b). Chamber posterior to body chamber small in mature specimens. Amphuncle dorsal, septal necks retrochoanitic extending to almost half a chamber in length.

Young stages impressed by three deep constrictions, these occupy the same relative positions on each whorl so that a pronounced triangular shape is produced. With age the constrictions weaken and finally disappear.

Ornament has not been seen on the Cornish specimens, but Schindewolf records occasional intensified growth lines which follow a straight course over the flanks and center. In addition, a slight spiral ornament has been recorded.

Genus *EPIWOCKLUMERIA* Schindewolf 1937 emend.

1937 *Epiwocklumeria* Schindewolf, p. 72.

Remarks. *Epiwocklumeria* was erected by Schindewolf using *Wocklumeria paradoxa* var. *applanata* Wedekind 1918 as the monogenotype. The affinities of *Epiwocklumeria* to the *Ionoclymeniaceae* were demonstrated; in the same work *Wocklumeria paradoxa* Wedekind, which was referred to the genus *Parawocklumeria* Schindewolf (1926), was placed in the *Parawocklumeriaceae*.

On the basis of the suture-line a new Cornish species belongs to the genus *Epiwocklumeria*, but it has several characters of *Parawocklumeria*, including a subglobose shape and straight constrictions; features thought by Schindewolf to be of generic importance. The addition of the new species requires modification of the generic diagnosis.

Emended diagnosis. A genus of the *Wocklumeriidae* with discoidal to globose form, shell broadly triangular in outline, the sides and venter impressed by three strong constrictions. Umbilicus almost closed. Ventral lobe of suture line deep, pointed; first lateral saddle rounded passing into an open V-shaped first lateral lobe. Second lateral saddle gently rounded, umbilical lobe shallow, divided at the umbilical seam by a small saddle. Dorsal lobe broad, V-shaped. First and second dorso-lateral saddles rounded, separated by a rounded dorso-lateral lobe.

Comparison with other genera. This genus resembles *Wocklumeria* on the basis of the suture-line, but differs in the very small size of the umbilicus, the more compressed form, and the absence of several contrasting stages during development. *Epiwocklumeria* shows a marked superficial similarity to *Parawocklumeria* but it has a fundamentally different suture-line.

Epiwocklumeria dunhevedensis sp. nov.

Plate 26, figs. 6, 7; text-fig. 2

Derivation of name. After Dunheved, the ancient name of Launceston.*Holotype.* GSM 87038, Pl. 26, figs. 6, 7, text-fig. 2.*Type locality.* Stourscombe (West Quarry), nr. Launceston.*Horizon.* Stourscombe Beds (Upper faunal division).*Material.* Only a single internal mould known.*Diagnosis.* Shell subglobose, triangular in outline, the sides and venter impressed by three pronounced constrictions. Umbilicus almost closed. Suture-line typical of the genus, the ventral lobe being shallow and rounded.*Description.* Species of *Epiwocklumeria* with subglobose shell, involute, greatest thickness at the umbilicus; involution almost entire, umbilicus minute, deep, and triangular.TEXT-FIG. 2. *Epiwocklumeria dunhevedensis* sp. nov.; holotype, GSM 87038, suture-line at 16 mm diameter.

in outline. Laterally whorls moderately compressed, strongly rounded ventrally; greatly impressed by the preceding whorl. Flanks marked by three constrictions following a straight course from the umbilicus to the periphery, being gently arched forwards over the venter. Body chamber approaches one whorl in length. External suture (text-fig. 2) typical of the genus; ventral lobe small, rounded. First lateral saddle pronounced, passing into a pointed, deep first lateral lobe. Second lateral lobe broadly rounded, passing into rounded umbilical lobe. No ornament has been observed.

Measurements of holotype (in mm.). D. 17, W.H. 8, W.T. 11, U. 1.*Comparisons.* This species differs from *Epiwocklumeria applanata* in the greater whorl thickness, the straight course of the constrictions over the whorl sides, and the size of the ventral lobe. Were it not for the characteristic suture line it would be difficult to distinguish this species from *Parawocklumeria laevigata* sp. nov.

Family GLATZIELLIDAE Schindewolf 1928

Genus POSTGLATZIELLA Schindewolf 1937

Postglatziella carinata Schindewolf 1937

Plate 26, figs. 8, 9

1937 *Postglatziella carinata* Schindewolf, p. 82, pl. 3, figs. 4-7, text-figs. 19a, b.*Remarks.* The few specimens from Stourscombe referable to this species differ from Schindewolf's specimens only in having the ribs more widely spaced.

Family CLYMENIIDAE Edwards 1849

Genus PLATYCLYMENIA Hyatt 1884

Platyclymenia (Platyclymenia) valida (Phillips 1841)

Plate 26, fig. 10

1841 *Clymenia valida* Phillips, p. 126, pl. 54, fig. 245.non 1914 *Platyclymenia valida* Wedekind, p. 37, pl. 3, figs. 3, 4.non 1956 *Platyclymenia (Platyclymenia) valida* Müller, p. 70, pl. 2, fig. 10.*Holotype* (by monotypy). GSM 7176. Pl. 26, fig. 10.*Type locality*. Landlake Limestone Quarry, nr. Launceston.*Horizon*. Lower Petherwin Beds.

Diagnosis. *Platyclymenia* with wide umbilicus and strong, closely spaced ribs on the young whorls. Ribs on the later whorls weaken in intensity, broaden, and become widely spaced at the umbilicus; towards the venter these give rise to three to four weak secondary and intercalatory ribs. Whorl cross-section rectangular.

Description. Shell evolute, with only very slightly embracing whorls. Umbilicus large, moderately deep, in complete specimens probably exposing all of the inner whorls. Whorl flanks flattened, particularly in the mature shell; venter broadly rounded to flattened. Whorl cross-section rectangular, considerably higher than wide.

Ornament on the inner whorls comprises distinct, irregularly spaced concave ribs. Frequently two or three ribs apparently arise from an almost common origin, this gives an irregular, noded appearance to the umbilical rim. On the succeeding whorls the ribs weaken and become more regular and closely spaced. On the final part of the last whorl the ribs at the umbilicus become quite widely spaced and broadly rounded. Towards the venter these divide into three to four fine, but weak, sigmoidal ribs. The fine ribs, some of which appear to be intercalatory, arise from a slightly raised area at approximately the mid-point of the flanks; as a result a weak spiral line is produced. Suture-line (Phillips 1841, p. 126, pl. 54, fig. 245*b*) typical of the genus.

Measurements of holotype (in mm.). D. 40, W.H. 13, W.T. 6, U. 18.

Remarks. The specimens figured and described by Wedekind (1914, p. 37, pl. 3, figs. 3, 4) as *Platyclymenia valida* (Phillips) lack the characteristic bifurcating ribs of the holotype, and appear to represent a new species not recorded from the Petherwin Beds. There are other records of the occurrence of the species in Germany which are unaccompanied by figures (Schindewolf 1923, Lange 1929, Matern 1931, Freyer 1957); it seems probable from the descriptions that reference was being made to the descriptions and figures of Wedekind rather than to those of Phillips.

Platyclymenia (Platyclymenia) bicostata Wedekind 19141914 *Platyclymenia bicostata* Wedekind, p. 36, pl. 3, figs. 16–18.1923 *Platyclymenia bicostata* Schindewolf, p. 450.1927 *Platyclymenia bicostata* Schlosser, p. 5, fig. 21.1931 *Platyclymenia bicostata* Matern, p. 100.1957 *Platyclymenia bicostata* Freyer, p. 56.

Remarks. A single specimen of this species is recorded from the Landlake Limestone Quarry. This specimen shows the characteristic paired ribs of the species. The posterior member of each pair of ribs is normally more strongly developed than the anterior. In the mature whorls the intensity of the ribbing decreases; a fragment of the latest whorl preserved appears to be almost smooth.

Platyclymenia (Platyclymenia) pattisoni (M'Coy 1851)

Plate 26, fig. 11.

- 1851 *Clymenia pattisoni* M'Coy, p. 488.
 1852 *Clymenia pattisoni* M'Coy, p. 403, pl. 2A, fig. 11.
 1854 *Clymenia pattisoni* M'Coy, p. 293.
 1855 *Clymenia subnautilina* Sandberger, p. 5, pl. 1, figs. 1a-f.
 1910 *Clymenia pseudoflexuosa* Rzehak, p. 181, pl. 1, fig. 1, pl. 2, figs. 8, 9.
 1914 *Platyclymenia quenstedti* Wedekind, p. 45, pl. 3, fig. 10, pl. 2, fig. 5.
 1922 *Platyclymenia subnautilina* (- *Platyclymenia quenstedti*) H. Schmidt in Kegel, p. 39.
 1923 *Platyclymenia quenstedti* Schindewolf, p. 457, text-fig. 19a.
 1929 *Platyclymenia (Varioclymenia) subnautilina* Lange, p. 102.
 1931 *Platyclymenia quenstedti quenstedti* Matern, p. 102.
 1950 *Platyclymenia quenstedti* G. & H. Termier, p. 74, pl. 154, figs. 8-11; pl. 157, figs. 31-33; pl. 161, figs. 18-20.
 1956 *Platyclymenia (Platyclymenia) subnautilina* Müller, p. 73.

Holotype (by monotypy). SMC H990. Pl. 26, fig. 11.

Type locality. Landlake Limestone Quarry, nr. Launceston.

Horizon. Lower Petherwin Beds.

Remarks. *Clymenia pattisoni* M'Coy was referred by Gümbel (1863, p. 126) to *Clymenia flexuosa* Münster (1840). However, it is quite distinct from this species, for *C. pattisoni* has a suture-line characteristic of the genus *Platyclymenia*, whereas *C. flexuosa* has a suture-line typical of the genus *Kosmoclymenia*.

M'Coy's species is identical to *P. (Platyclymenia) subnautilina* (Sandberger) and its junior synonyms *P. (Platyclymenia) quenstedti* Wedekind, and *Clymenia pseudoflexuosa* Rzehak. Sandberger's original figures are good and Schmidt's synonymy appears quite

EXPLANATION OF PLATE 26

- Fig. 1. *Costaclymenia muensteri* (Ansted), Landlake Limestone Quarry. Holotype, SMC H4010, $\times 1$.
 Fig. 2. *Gonioclymenia (Kalloclymenia) biimpressa* (von Buch), Landlake Limestone Quarry. GSM 7083, $\times 1$.
 Figs. 3-5. *Wocklumeria sphaeroides* (Rh. Richter), Stourscombe. 3, 4, Lateral and ventral view of mature individual showing the change in spiral angle of the anterior part of the body chamber and the apertural constriction, GSM 87033, $\times 1$. 5, Young specimen showing constrictions and triangular-shaped umbilicus, GSM 87037, $\times 2$.
 Figs. 6, 7. *Epiwocklumeria dunhevedensis* sp. nov., Stourscombe. Holotype, GSM 87038. 6, Lateral view showing straight constrictions, $\times 2$. 7, Ventral view showing suture-line, $\times 1\frac{1}{2}$.
 Figs. 8, 9. *Postglatziella carinata* Schindewolf, Stourscombe. 8, GSM 87040, $\times 2$. 9, GSM 87039, $\times 3$.
 Fig. 10. *Platyclymenia (Platyclymenia) valida* (Phillips), Landlake Limestone Quarry. Holotype, GSM 7176, $\times 1$.
 Fig. 11. *Platyclymenia (Platyclymenia) pattisoni* (M'Coy), Landlake Limestone Quarry. Holotype, SMC H990, $\times 2$.
 Fig. 12. *Kosmoclymenia linearis* (Münster), Stourscombe. GSM 87042, $\times 1$.



valid and was confirmed by Lange (1929) and by Müller (1956). The identity of *Platyclymenia pattisoni* with these species means that *Platyclymenia subnautilina* must now be reduced to a synonym of the Cornish species; the name of which has a priority of several years.

Measurements of holotype (in mm.). D. 20, W.H. 7, W.T. 5, U. 9.5.

Genus KOSMOCLYMENIA Schindewolf 1949

Kosmoclymenia pattisoni sp. nov.

Plate 27, fig. 1

Derivation of name. After Mr. S. R. Pattison, an early pioneer in Launceston geology.

Holotype. GSM 87043. Pl. 27, fig. 1.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds (Lower faunal division).

Material. A single specimen showing both suture- and growth-lines.

Diagnosis. *Kosmoclymenia* with disk-shaped shell, umbilicus wide, deep for genus. Initially the whorls increase slowly in size, but the last $1\frac{1}{2}$ whorls increase rapidly. Whorl height exceeds whorl thickness. Ornament consists of pronounced, raised growth lines.

Description. Shell evolute, planorbiform, with seven to eight very slightly embracing whorls. Umbilicus large, relatively deep, exposing all of the inner whorls. Up to a diameter of 2–3 mm. whorl thickness may equal whorl height, thereafter whorl height always exceeds whorl thickness. Venter broadly rounded. Initial increase in whorl size slight; last $1\frac{1}{2}$ whorls increasing very rapidly, almost doubling in height in the last whorl. In young stages whorl sides rounded, later whorls broadly rounded to flattened. The rapid increase in size of the final whorl creates a rather deeper umbilicus than is normal for the genus. Ornament composed of biconvex growth lines. Suture-line typical of the genus.

Comparisons. The general appearance of the shell is similar to *K. wocklumeri*, but the flanks are not so flattened and they do not converge to a flattened venter. The ornament is also much stronger than in this species. *K. linearis* is characterized by a slow increase in the size of the whorl, and in consequence the umbilicus is very shallow. *K. sedgwicki* is more compressed and involuted than this species.

Measurements of holotype (in mm.). D. 50, W.H. 18, W.T. 14, U. 22.

Family CYRTOCLYMENIIDAE Hyatt 1884

Genus CYRTOCLYMENIA Hyatt 1884

Cyrtoclymenia tetragona Schmidt 1924

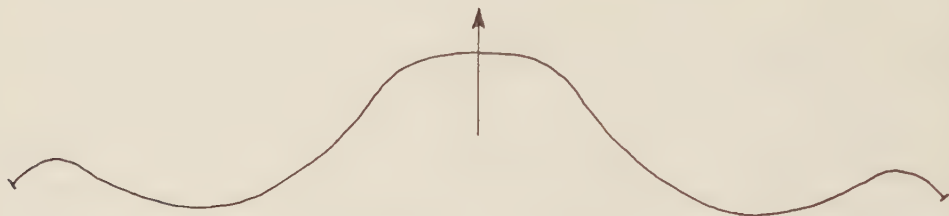
Plate 27, fig. 11; text-fig. 3

1924 *Cyrtoclymenia tetragona* Schmidt, p. 127, pl. 6, figs. 22, 23.

Remarks. Specimens from Cornwall agree closely with the original description, and exhibit details of the suture-line not previously recorded. Just posterior to the body

chamber the septa are crowded, but they become more widely spaced posteriorly. The suture-line consists of a pronounced, rather flattened, ventral saddle which passes into a broad, shallow lateral lobe. A weak lobe is developed at the umbilicus. A geniculate constriction mid-way along the body chamber is present on one specimen. The specimen figured is less globose than that illustrated by Schmidt.

Measurements of figured specimen (GSM 87044) (in mm.). D. 27·5, W.H. 13·5, W.T. 10·5, U. 4·5.



TEXT-FIG. 3. *Cyrtoclymenia tetragona* Schmidt; GSM 87044, suture-line at 26 mm. diameter.

Genus CYMACLYMENIA Hyatt 1884

Cymaclymenia striata var.

Plate 27, figs. 3, 4

Remarks. A number of specimens differ from *C. striata* (Münster 1832). The whorl thickness of these specimens is greater and the involution is considerable; the umbilicus only amounts to one-seventh of the shell diameter. This variety has only been found in the lower faunal division at Stourscombe.

Cymaclymenia constricta sp. nov.

Plate 27, figs. 8-10

Derivation of name. After the constrictions on the venter.

Holotype. GSM 87050. Pl. 27, figs. 8, 9.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds.

Material. Internal and external moulds.

Diagnosis. Discoidal *Cymaclymenia* with narrow umbilicus. Flanks and venter rather flattened; venter shows pronounced sinuate constrictions.

Description. Shell discoidal, involute, umbilicus narrow and deep but exposing all of the inner whorls. Whorl section rather compressed, whorl height just exceeding whorl thickness. Venter broadly rounded, becoming flattened in mature specimens; clearly marked by periodic sinuate constrictions which do not continue on to the flanks. Constrictions closely spaced in young specimens but more widely spaced in adult forms. Whorl flanks flattened at maturity, though broadly rounded in youth; tending to converge towards the venter. Final whorl increases rapidly in size, involution of this whorl

two-thirds to four-fifths. Suture-line typical of the genus, though the ventral saddle is not well developed; eight to nine chambers per whorl. Preservation of the material is not delicate enough for growth lines to be preserved.

Measurements of holotype (in mm.). D. 17, W.H. 10, W.T. 7.5, U. 4.

Comparisons. The presence of constrictions is not a particularly common feature of this genus. *Clymenia semistriata* Münster (1832) exhibits constrictions over the flanks, but these are absent over the venter. The specimen figured by Münster (1840) as *Clymenia dorsocostata* appears to show constrictions over the venter, but these are much more closely spaced, and weaker, than those shown by the Cornish specimens, and appear to be produced by raised growth-lines.

Cymaclymenia constricta sp. nov. var. A

Plate 27, figs. 12, 13

Holotype. GSM 87052. Pl. 27, figs. 12, 13.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds (Lower faunal division).

Remarks. This variety shows more widely spaced and decidedly weaker constrictions on the venter at all growth stages. In addition the increase in the size of the final whorl, and the amount of involution is not so great.

Measurements of holotype (in mm.). D. 32, W.H. 16, W.T. 12.5, U. 6.5.

Cymaclymenia constricta sp. nov. var. *globosa* nov.

Plate 27, figs. 14, 15

Holotype. GSM 87051. Pl. 27, figs. 14, 15.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds (Lower faunal division).

Remarks. This variety, represented by a single specimen, shows a whorl thickness in excess of the whorl height; thus the shell is more globose than is normal for the species. The venter is strongly rounded and the first constrictions do not develop until a diameter of 13.5 mm. is reached.

Measurements of holotype (in mm.). D. 16.5, W.H. 8, W.T. 8.5, U. 4.

Family PARAWOCKLUMERIIDAE Schindewolf 1937

Genus PARAWOCKLUMERIA Schindewolf 1926

Parawocklumeria laevigata sp. nov.

Plate 27, figs. 16–20; text-fig. 4A

Derivation of name. After the smooth shell.

Holotype. GSM 87053. Pl. 27, figs. 18, 19.

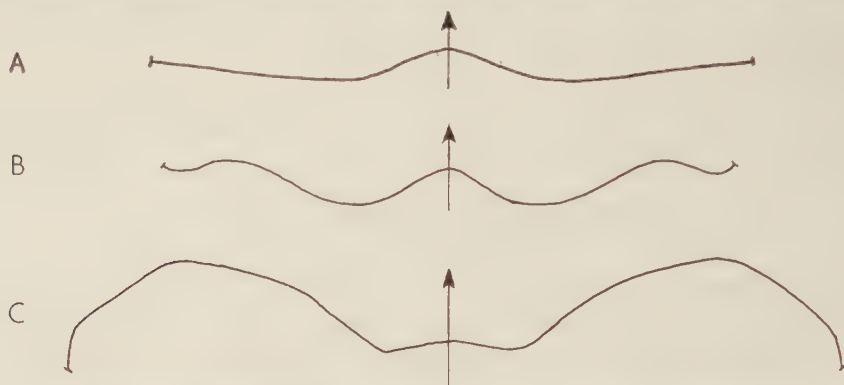
Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds (Lower faunal division).

Material. Internal and external moulds.

Diagnosis. *Parawocklumeria* with discoidal to subglobose shell; umbilicus narrow, of triangular shape. Three strong constrictions give a pronounced trilobation to the shell. Ornament absent. Suture-line variable.

Description. Shell discoidal to subglobose, involute, greatest thickness at the umbilicus. Five to six whorls, involution almost complete. Umbilicus minute, deep, and triangular

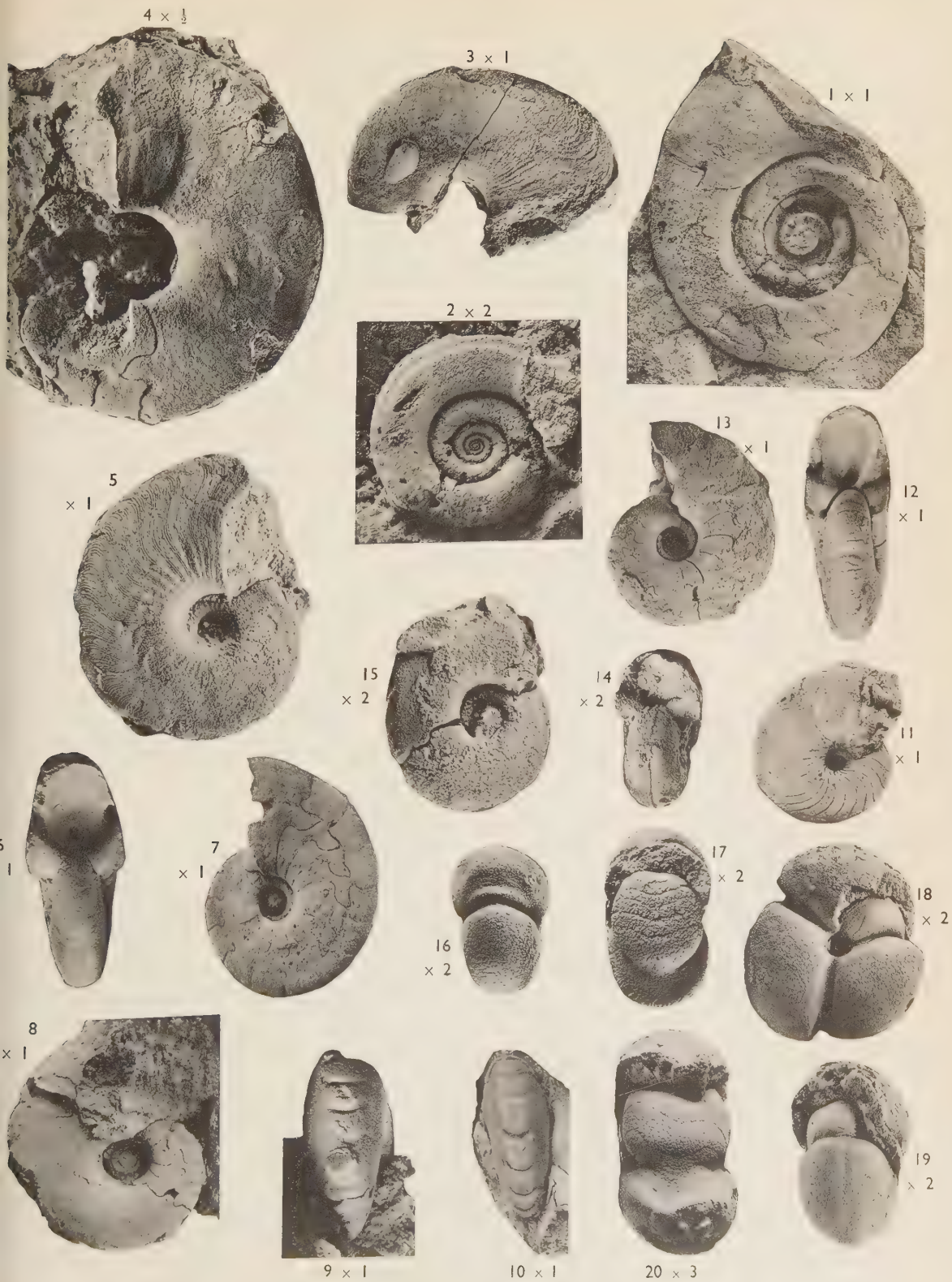


TEXT-FIG. 4. A, *Parawocklumeria laevigata* sp. nov.; GSM 87054, suture-line at 9 mm. diameter. B, *Parawocklumeria laevigata* sp. nov. var. *obesa* nov.; holotype, GSM 87088, suture-line at 6.5 mm. diameter. C, *Parawocklumeria* sp.; GSM 87057, suture-line at 10 mm. diameter.

in shape. Whorls laterally compressed, strongly rounded ventrally, greatly impressed by the preceding whorl. Flanks marked by three deep constrictions, occupying the same relative position on each successive whorl. Constriction straight and radial on the flanks, swinging weakly forward over the venter. Shallow secondary constrictions, broader than the main constrictions and present only over the venter, occur anterior to

EXPLANATION OF PLATE 27

- Fig. 1. *Kosmoclymenia pattisoni* sp. nov., Stourscombe. Holotype, GSM 87043, $\times 1$.
 Fig. 2. *Kosmoclymenia bisulcata* (Münster), Stourscombe. GSM 87041, $\times 2$.
 Figs. 3, 4. *Cymaclymenia striata* var., Stourscombe. 3, specimen showing growth-lines, GSM 87046, $\times 1$. 4, GSM 87045, $\times \frac{1}{2}$.
 Fig. 5. *Cymaclymenia cordata* Wedekind, Stourscombe. GSM 87047, $\times 1$.
 Figs. 6, 7. *Cymaclymenia camerata* Schindewolf, Stourscombe. Ventral and lateral view, GSM 87048, $\times 1$.
 Figs. 8–10. *Cymaclymenia constricta* sp. nov., Stourscombe. 8, Lateral view of holotype, GSM 87050, $\times 1$. 9, Ventral view of holotype showing constrictions on the venter, GSM 87050, $\times 1$. 10, Ventral view of specimen with rather flattened venter, GSM 87049, $\times 1$.
 Fig. 11. *Cyrtoclymenia tetragona* Schmidt, Stourscombe, GSM 87044, $\times 1$.
 Figs. 12, 13. *Cymaclymenia constricta* var. A, Stourscombe. Ventral and lateral view, GSM 87052, $\times 1$.
 Figs. 14, 15. *Cymaclymenia constricta* var. *globosa* var. nov., Stourscombe. Lateral and ventral view, GSM 87051, $\times 2$. The final part of the last whorl has been removed in fig. 14 to show the characteristic whorl cross-section.
 Figs. 16–20. *Parawocklumeria laevigata* sp. nov., Stourscombe. 16, Ventral view showing secondary constriction lying just anterior to the main constriction on the venter, GSM 87055, $\times 2$. 17, Ventral view of mature individual showing closely spaced suture-lines just posterior to the body chamber, GSM 87054, $\times 2$. 18, 19, Lateral and ventral view of holotype, GSM 87053, $\times 2$. 20, Specimen showing asymmetrical suture-lines, GSM 87056, $\times 3$.



the main constrictions in some internal moulds. A median furrow is occasionally preserved extending between the constrictions on the internal moulds of some specimens (Pl. 27, fig. 19). Body chamber 1–1½ whorls. In mature specimens the final suture-lines become progressively more closely spaced. Siphuncle dorsal, septal necks retrochoanitic. External suture-line (text-fig. 4A) variable; ventral saddle broadly rounded passing into a very shallow lateral lobe and saddle. Umbilical lobe frequently not developed. Suture-line often asymmetrical in form (Pl. 27, fig. 20).

Measurements of holotype (in mm.). D. 16, W.H. 7, W.T. 10, U. 2.

Comparisons. Only *P. paradoxa* (Wedekind) bears comparison with the species. The marked ornament on the German species is absent in *P. laevigata*, and in addition the umbilicus of the Cornish species is wider and the ventral saddle of the suture line is less pronounced. Secondary constrictions are not present in *P. paradoxa*.

Parawocklumeria laevigata sp. nov. var. *obesa* nov.

Plate 28, figs. 1, 2; text-fig. 4B

Derivation of name. After globose shell.

Holotype. GSM 87088. Pl. 28, figs. 1, 2.

Type locality and horizon. As for *P. laevigata*.

Material. Internal and external moulds.

Diagnosis. Globose variety of the species possessing a suture-line closely resembling *P. paradoxa* (Wedekind).

Measurements of holotype (in mm.). D. 8, W.H. 4, W.T. 7.5, U. 0.75.

Comparisons. *P. laevigata* var. *obesa* is very similar to *P. laevigata*, and though it is somewhat more globose, the essential difference lies in the nature of the suture-line (text-fig. 4B) which is much more elaborated both in young and adult forms.

Parawocklumeria sp.

Plate 28, fig. 3; text-fig. 4C

Description. A single specimen of *Parawocklumeria* from the lower faunal horizon in the West Quarry at Stourcombe has a subglobose shell of similar form to *P. laevigata*. The suture-line is, however, distinctive, being characterized by an exceedingly small ventral saddle which follows the anterior arching of the constriction over the venter. The lateral lobe is shallow and passes into a pronounced lateral saddle. The umbilical lobe lies at the umbilical seam. Umbilicus deep, moderately small, and of triangular shape. No ornament has been observed.

Measurements. D. 10.5, W.H. 4.5, W.T. 7, U. 1.5.

Family CHEILO CERATIDAE Frech 1897

Genus KENSEYOCERAS gen. nov.

Derivation of name. After the River Kensey.

Type species. *Kenseyoceras* (*Kenseyoceras*) *rostrata* sp. nov.

Range. Upper Devonian. *Wocklumeria* Zone (V1).

Diagnosis. Shell discoidal to subglobose, completely involute. Flanks marked by deep radial constrictions which swing forwards at the venter to form grooves bounding a median keel. Suture-line consists of a ventral saddle divided by a deep parallel-sided lobe, lateral lobe bell shaped passing into a gently arched lateral saddle.

Comparisons. Two species *K. (Kensyoceras) biforme* (Schindewolf 1937) and *K. (Mayneoceras) nucleus* (Schmidt 1924), now placed in this genus, were referred to the genus *Prionoceras* by Schindewolf (1937). *Prionoceras* is alleged to show a suture-line with a prolobitid development; a feature which would place the above species in the Prolobitidae. However, it has never been conclusively demonstrated that *Prionoceras* has a prolobitid suture-line, and *P. biforme* and *P. nucleus* were referred to the genus without reference to the development of their suture-lines. If *Prionoceras* is found to lack the prolobitid suture then it almost certainly becomes a member of the Cheiloceratidae and indistinguishable from *Imitoceras* (*Treatise on Invertebrate Paleontology*, p. L50). It has not been possible to break the shells of species of *Kensyoceras* completely down to the protoconchs, but the earliest sutures examined have given no indication of a prolobitid suture-line development. The form of the suture-line makes closer reference to the Cheiloceratidae and to the subfamily Imitoceratinae in particular. Of the genera composing the Imitoceratinae *Kensyoceras* is most closely related to *Imitoceras*, but is distinguished from it by the presence of a raised keel bounded by spiral grooves.

Remarks. Schmidt (1924) figured two new species, *Glatziella nucleus* (p. 119, pl. 6, figs. 10, 10a, 11) and *Gattendorfia globularis* (p. 120, pl. 6, figs. 12, 12a, 13, 13a), from rocks at the Devonian–Carboniferous boundary in the Sauerland. In this work he failed to designate the holotypes of his new species. Lange (1929) observed that, apart from the suture-line, *Gattendorfia globularis* was quite distinct from other species of *Gattendorfia* and included it in a new subgenus, *Gattendorfia (Balvia)*. No lectotype was designated.

Schindewolf (1937, p. 15, footnote 1) noted that Schmidt had confused three species in the descriptions of *Gattendorfia globularis* and *Glatziella nucleus*, and reinterpreted Schmidt's figures thus:

Glatziella nucleus Schmidt (p. 119, pl. 6, figs. 10, 10a).

Gattendorfia globularis Schmidt (p. 120, pl. 6, figs. 13, 13a).

Prionoceras biforme n. sp. (pl. 6, figs. 11, 12, 12a; holotype figs. 12, 12a).

Schindewolf also (1937, p. 24, footnote 3) referred the revised species *Glatziella nucleus* to *Prionoceras*. The revised species *Gattendorfia globularis* becomes, on this new interpretation, a characteristic member of the genus *Gattendorfia*. Since there is no doubt that *G. globularis* represented the subgenotype of *G. (Balvia)* Lange, *Balvia* is reduced to a subjective synonym of *Gattendorfia* (not *Imitoceras* as is suggested in the *Treatise on Invertebrate Paleontology*, p. L49). A new genus is therefore proposed to include *P. biforme* and *P. nucleus*.

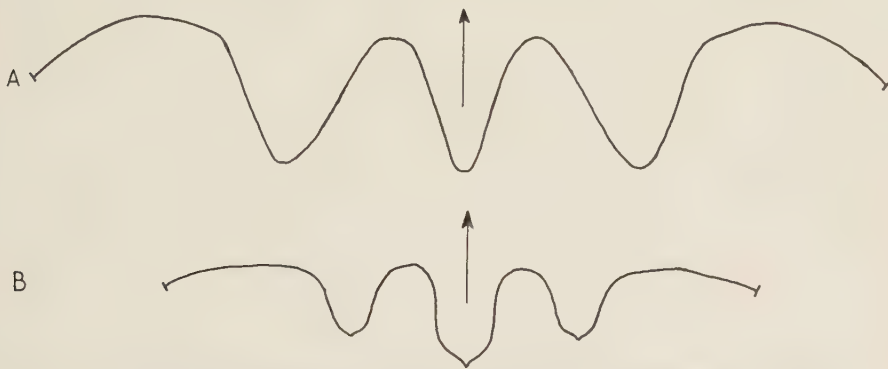
KENSEYOCERAS (KENSEYOCERAS) subgen. nov.

Diagnosis. Discoidal to subglobose. Final third of body chamber characterized by a median keel bounded by furrows. Keel carried forwards to form a pronounced rostrum. Apertural modification terminated posteriorly by constrictions which cross the flanks and reach to the umbilicus.

KENSEYOCERAS (MAYNEOCERAS) subgen. nov.

Derivation of name. After Cuthbert Mayne, a Launceston martyr.

Diagnosis. Discoidal *Kenseyoceras* with pronounced constrictions over the flanks which cross the venter in youth, but later pass into sulci bordering a median keel.



TEXT-FIG. 5. A, *Kenseyoceras (Kenseyoceras) rostrata* sp. nov.; GSM 87059, suture-line at 9 mm. diameter. B, *Kenseyoceras (Mayneoceras) nucleus* (Schmidt); GSM 87068, suture-line at 7 mm. diameter.

Kenseyoceras (Kenseyoceras) rostrata sp. nov.

Plate 28, figs. 4–10; text-fig. 5A

Derivation of name. After the pronounced rostrum.

Holotype. GSM 87058. Pl. 28, fig. 4.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds.

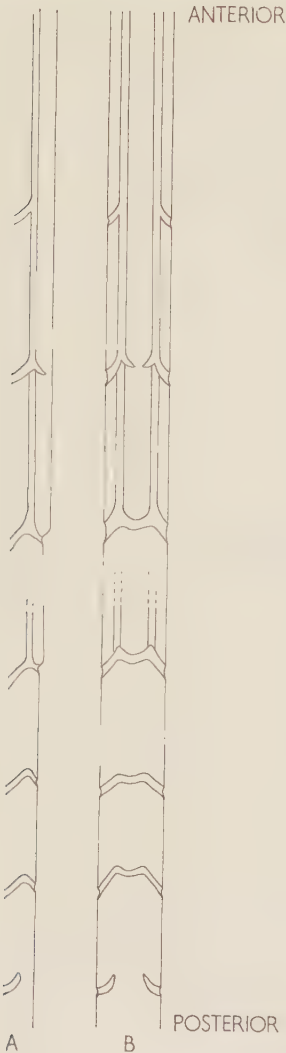
Material. Internal and external moulds.

Diagnosis. Shell discoidal to subglobose, anterior portion of body chamber with a pronounced keel, terminated posteriorly by a tubercle, and bounded by grooves which posteriorly cross the flanks as constrictions reaching to the umbilicus. Keel and sulci reduced anteriorly to form a broad rostrum.

Description. Shell discoidal to subglobose, involute, greatest thickness at the umbilicus. Five to six whorls, inclusion complete; umbilicus closed and depressed. Whorls slightly compressed laterally, strongly rounded ventrally, flanks moderately convex; whorls deeply impressed by the preceding whorl, aperture height small. Body chamber just exceeds one volution. Suture-lines closely spaced just posterior to the body chamber (Pl. 28, fig. 8). External suture-line consisting of deep and pointed ventral lobe. First lateral saddle acutely rounded, passing into a broad V-shaped first lateral lobe; second lateral saddle broadly arched, passing into moderately deep umbilical lobe.

On the last third of the body chamber a pair of constrictions, deeply concave to the anterior, extend from the umbilicus towards the periphery attaining maximum concavity one-third of the distance from the venter. From this point each is carried forward,

just off the venter, forming two deep sulci separated by a raised, slightly corded keel.



TEXT-FIG. 6. *Kenseyoceras* (*Mayneoceras*) *nucleus* Schmidt. Diagrams illustrating the successive stages in the development of the keel. A, Lateral view. B, Ventral view. The diagrams represent the appearance of rather more than two whorls if they were to be uncoiled.

The sulci are continued into a rostrum where the free end of the keel is terminated in a small, hyponomic sinus; the proximal end of the keel is marked by a tubercle. A second, less prominent pair of constrictions, similar to, but less concave than the former, occupy a position just posterior to the aperture. Fine ornament is seldom preserved.

Measurements of holotype (in mm.). D. 10.5, W.H. 4.5, W.T. 6.5, U. closed.

Comparisons. This species is comparable to *Prionoceras biforme* Schindewolf (see above); although no description of the species is given, Schindewolf does select a holotype from Schmidt's figures. In the English species the rostrum maintains the whorl spiral, and the keel is more pronounced and terminated posteriorly by a tubercle. In addition, the pattern formed by the sulci at the posterior termination of the apertural modification is not so highly elaborated over the keel as that figured by Schmidt (1924, pl. 6, fig. 12).

Remarks. There appears to be a good deal of variation in the shape of the shell of this species which covers all gradations from discoidal to subglobose. In addition the tubercle at the posterior end of the keel is frequently not fully developed.

Kenseyoceras (*Mayneoceras*) *nucleus* (Schmidt 1924)

Plate 28, figs. 11–17; text-figs. 5B, 6

- 1924 *Glatziella nucleus* Schmidt, p. 119, pl. 6, figs. 10, 10a (non 11).
- 1929 ? *Prionoceras* or ? *Gattendorfia* (*Balvia*) *nucleus* Lange, p. 61, pars.
- 1937 *Prionoceras nucleus* Schindewolf, p. 24, footnote 3.

Diagnosis. Shell discoidal. Flanks impressed by three constrictions in youth, increasing to four or rarely five with age. Mature shell bears pronounced keel bounded by spiral grooves.

Description. Shell compressed, discoidal in shape, involute. Seven to eight whorls, inclusion complete; umbilicus closed. Whorls considerably compressed laterally, strongly rounded ventrally; whorls deeply impressed by the preceding volutions. Twelve to thirteen suture-lines per whorl.

these are closely spaced anteriorly. External suture-line (text-fig. 5B); ventral lobe deep parallel sided, first lateral saddle rounded, passing into moderately deep first lateral lobe

Second lateral saddle gently arched, passing into shallow umbilical lobe. Dorsal lobe deep and narrow.

In young forms whorl sides deeply impressed by three straight constrictions reaching from the umbilicus to the periphery. Initially the constrictions do not unite over the venter but are carried forwards, forming two short spiral grooves. In older specimens these grooves become united through the formation of a posteriorly arched furrow. Subsequently two spiral grooves, separated by a slightly raised keel, develop anteriorly to the constrictions. At first the keel and grooves fail to persist from one constriction to the next, but later become continuous. When this condition is established the constriction pattern over the venter weakens and finally disappears; the lateral constrictions merging into the spiral grooves. No fine ornament has been observed on the Cornish specimens.

In the early stages a suture-line often coincides with a constriction; the ventral lobe of the suture is then much deeper than the constriction sinus.

The adult shell bears four or rarely five constrictions.

Kenseyoceras (Mayneoceras) sinuconstricta sp. nov.

Plate 28, figs. 18–20

Derivation of name. After the sigmoidally curved constrictions.

Holotype. GSM 87069. Pl. 28, figs. 18–20.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds.

Material. Internal and external moulds.

Diagnosis. Discoidal to subglobose *K. (Mayneoceras)* with flattened venter and parallel-sided flanks. Flanks impressed by three sigmoidally curved constrictions.

Description. Shell discoidal to subglobose, involute; greatest thickness at the umbilicus. Six to seven whorls, inclusion complete; umbilicus closed. Shell considerably compressed laterally, flattened ventrally, flanks parallel-sided. Each whorl considerably impressed by the preceding whorl. Body chamber just exceeds one whorl. Suture-line typical of the genus.

Flanks deeply impressed by three sigmoidally curved constrictions; the intensity of the constrictions increasing towards the venter. Over the venter constrictions show a well-developed median sulcus separating two equally developed lobes. In mature specimens a median keel develops anterior to the last constriction, this keel is bounded by grooves.

Measurements of holotype (in mm.). D. 11, W.H. 6, W.T. 6.5, U. closed.

Comparisons. This species may be distinguished from *K. (Mayneoceras) nucleus* by its thicker whorl cross-section, flattened venter, and by the sinuous pattern of the constrictions over the flanks.

Genus SPORADOCERAS Hyatt 1884

Sporadoceras orbiculare var.

Plate 29, figs. 1, 2; text-fig. 7

Remarks. The suture-line of this variety (text-fig. 7) differs from that described for the species. The lobes are narrow and of unusual depth for the species.



TEXT-FIG. 7. *Sporadoceras orbiculare* var.; GSM 87074, suture-line at 47 mm. diameter.

Genus DISCOCLYMENIA Hyatt 1884

Discoclymenia cornwallensis sp. nov.

Plate 28, figs. 22, 23; text-fig. 8

Derivation of name. After the county of Cornwall.

Holotype. GSM 87071. Pl. 28, fig. 22; text-fig. 8.

Type locality. Stourscombe (West Quarry), nr. Launceston.

Horizon. Stourscombe Beds.

Material. Internal and external moulds.

EXPLANATION OF PLATE 28

Figs. 1, 2. *Parawocklumeria laevigata* sp. nov. var. *obesa* nov. Stourscombe. Ventral and lateral view of holotype, GSM 87088, $\times 3$.

Fig. 3. *Parawocklumeria* sp. Stourscombe. GSM 87057, $\times 3$.

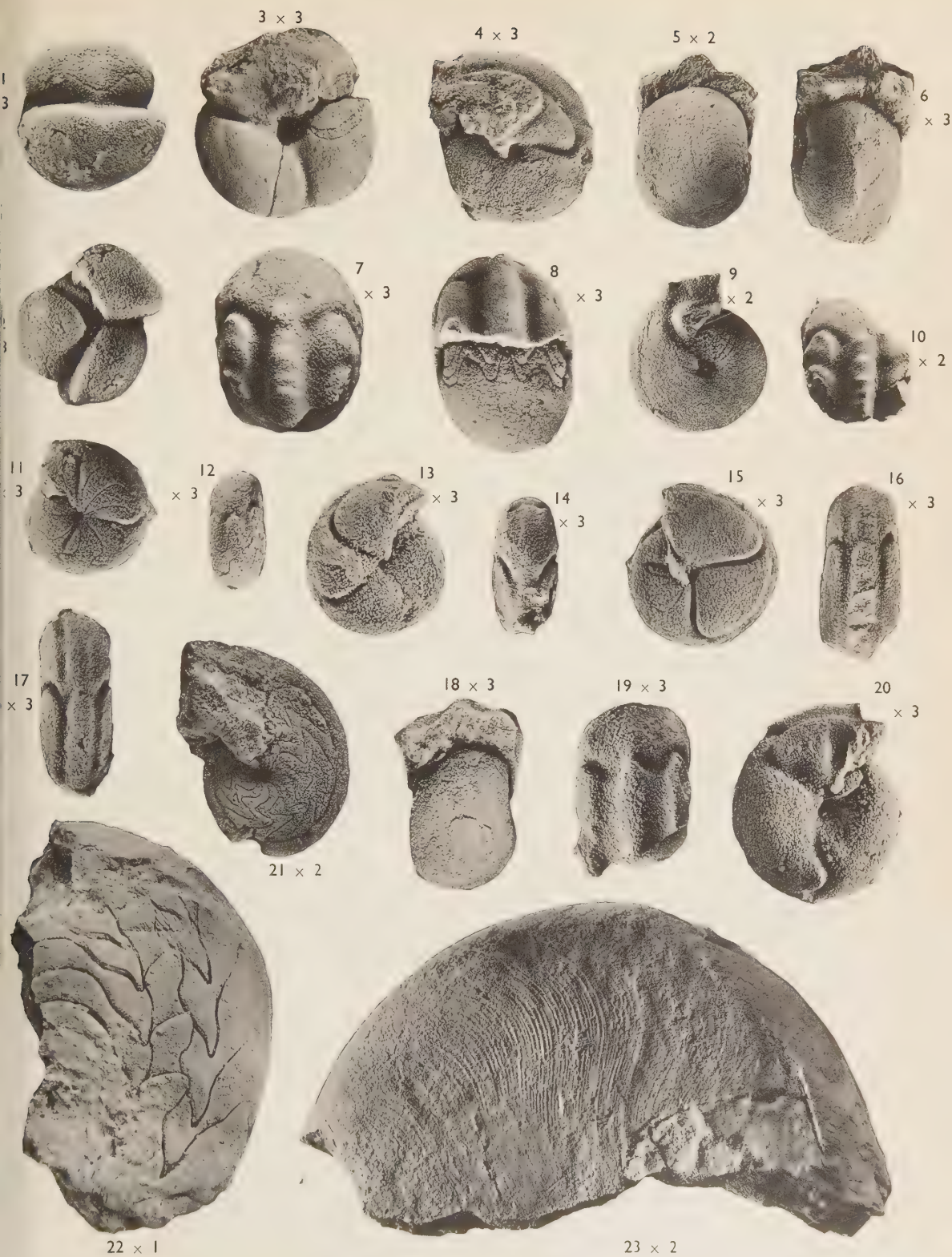
Figs. 4–10. *Kenseyoceras* (*Kenseyoceras*) *rostrata* gen. and sp. nov., Stourscombe. 4, Lateral view of holotype showing apertural modification, GSM 87058, $\times 3$. 5, GSM 87061, $\times 2$, and 6, GSM 87062, $\times 3$, ventral views showing variation in whorl thickness. 7, 8, Specimen viewed from above showing posterior termination of the apertural modification and suture-line, GSM 87059, $\times 3$. 9, Specimen showing tubercle at posterior termination of keel, GSM 87063, $\times 2$. 10, Fragment showing corded keel, GSM 87060, $\times 2$.

Figs. 11–17. *Kenseyoceras* (*Mayneoceras*) *nucleus* Schmidt, Stourscombe. 11, 12, Lateral and ventral view of young specimen showing suture-line and three constrictions which do not unite over the venter, GSM 87068, $\times 3$. 13, 14, Lateral and ventral view of slightly older specimen showing four constrictions almost uniting over the venter, GSM 87065, $\times 3$. 15, 16, Lateral and ventral view showing the keel developing between two spiral grooves, GSM 87064, $\times 3$. 17, Ventral view showing almost continuous spiral grooves between the constrictions and weakening of the constriction over the venter, GSM 87066, $\times 3$.

Figs. 18–20. *Kenseyoceras* (*Mayneoceras*) *sinuconstricta* sp. nov. Stourscombe. Ventral and lateral view of holotype, GSM 87069, $\times 3$.

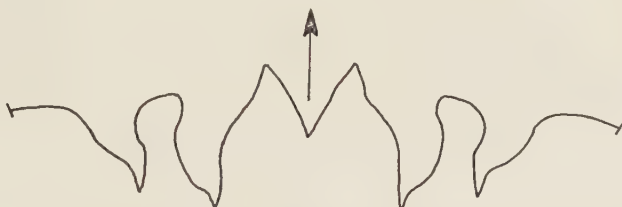
Fig. 21. *Discoclymenia cucullata* (von Buch) Stourscombe. GSM 87070, $\times 2$.

Figs. 22, 23. *Discoclymenia cornwallensis* sp. nov. Stourscombe. 22, Lateral view of holotype showing suture-lines in contact, GSM 87071, $\times 1$. 23, Specimen showing growth-lines, GSM 87072, $\times 2$.



Diagnosis. Thickly discoidal *Discoclymenia* with convex growth-lines. The suture-line has a broad V-shaped ventral lobe, and a pointed first lateral saddle bearing on its dorsal side a very flat adventitious lobe.

Description. Shell thickly discoidal; involute with closed umbilicus. Greatest thickness at the umbilicus. Whorl subquadrate in section, whorl height exceeding whorl thickness. Venter broadly convex, flanks flattened, converging slightly towards the venter. Growth-lines convex, fine and closely spaced. Constrictions not seen.



TEXT-FIG. 8. *Discoclymenia cornwallensis* sp. nov.; holotype, GSM 87071, suture-line at a whorl height of 36 mm.

Suture-line (text-fig. 8). Ventral lobe of broad V shape. First lateral saddle pointed, bearing on its dorsal side a very flat, adventitious lobe. First lateral lobe asymmetrical, deep, and pointed. Second lateral saddle rounded, directed upwards towards the venter. Second lateral lobe asymmetrical, broad, and pointed, with almost straight ventral surface; dorsal surface undulatory, passing into a gently arched umbilical saddle.

Measurements of holotype (in mm.). W.H. 36, W.T. 28.

Remarks. A feature of the figured specimen is the closely spaced nature of the suture-lines, and the manner in which the first lateral saddles of each suture are in contact. In one instance the first lateral lobe seems to have been interrupted by the first lateral saddle of the preceding suture.

Comparisons. The suture-line of this species is comparable to *Discoclymenia* sp. of Müller (1956, p. 62), differing only in the size of the ventral lobe; in Müller's species this is narrow and parallel sided. The adventitious lobe in *D. cucullata* (von Buch 1839) is more strongly developed than in *D. cornwallensis*.

Discoclymenia aff. *cornwallensis* sp. nov.

Plate 29, fig. 3

Remarks. This form is similar to *D. cornwallensis*, but it shows a slightly different suture-line. This is not so elaborated and shows the smoother form more generally associated with *Sporadoceras*; in addition the ventral lobe is deep and parallel sided.

Genus *GATTENDORFIA* Schindewolf 1920*Gattendorfia crassa* H. Schmidt 19241940 *Gattendorfia crassa* Librovitch, p. 45, pl. 4, figs. 1-4 (with full synonymy).1952 *Gattendorfia crassa* Schindewolf, p. 296, text-figs. 16, 17.1954 *Gattendorfia crassa* Pfeiffer, p. 57, pl. 7, fig. 3.1955 *Gattendorfia crassa* Goldring, p. 48.*Comparison with described forms* (measurements in mm.)

Specimen	D.	W.T.	W.T. %D.	W.H.	W.H. %D.	U.	U. %D.
1952	46.0	37.0	60	22.0	47	10.5	22
BU 12883	10.0	7.0	70	5.0	50	2.5	25

Gattendorfia occlusa Librovitch 19401940 *Gattendorfia occlusa* Librovitch, p. 237, pl. 6, figs. 5, 6, text-figs. 16, 17.*Comparison with described forms* (measurements in mm.)

Specimen	D.	W.T.	W.T. %D.	W.H.	W.H. %D.	U.	U. %D.
1940 (holotype) . . .	31.0	15.0	46	18.0	58	3.0	9
Range	..	..	41-62	..	46-58	..	9-17
BU 12884	12.5	5.5	44	6.0	48	2.0	16
BU 12915	8.5	3.0	35	3.5	41	1.0	11

Remarks. Two specimens from Penfoot show remarkably small umbilici. The proportions of these specimens are very close to those of *G. occlusa* from Kazakhstan; the specimens are referred to this species in preference to the involute European species *G. involuta* Schindewolf which is inadequately described.

Gattendorfia tenuis Schindewolf 19521952 *Gattendorfia tenuis* Schindewolf, p. 298, pl. 3, fig. 1, text-fig. 18.*Comparison with the holotype* (measurements in mm.)

Specimen	D.	W.T.	W.T. %D.	W.H.	W.H. %D.	U.	U. %D.
BU 12885	19	7	37	8	42	5	26
1952 (holotype) . . .	73	23	31	33	44	18	24

Remarks. The proportions of the Cornish specimen are close to those of the holotype but the shell has a slightly greater whorl thickness.

Gattendorfia subinvoluta (Münster 1839)1940 *Gattendorfia* cf. *subinvoluta* Librovitch, p. 40, pl. 3, figs. 6a, b (with full synonymy).1952 *Gattendorfia subinvoluta* Schindewolf, p. 295, text-fig. 15.

Comparison with described forms (measurements in mm.)

<i>Specimen</i>	<i>D.</i>	<i>W.T.</i>	<i>W.T. %D.</i>	<i>W.H.</i>	<i>W.H. %D.</i>	<i>U.</i>	<i>U. %D.</i>
1940	14.5	6.5	45	4.7	32	7.5	51
1952	52.0	24.0	46	19.0	37	16.0	30
BU 12886	18.0	6.0	33	6.5	36	7.0	39
BU 12887	20.5	8.5	41	7.0	33	9.0	43
BU 12888	13.0	6.5	50	4.5	34	6.0	46
BU 12889	19.0	6.0	31	5.5	29	7.5	39
BU 12890	18.0	6.0	33	6.0	33	8.0	44

Remarks. *G. subinvoluta* is the most commonly occurring Cornish species of this genus. Specimens collected show that the species is variable, particularly in whorl thickness. The Cornish specimens tend to be more evolute than forms described from Germany, for the umbilicus has a size range most comparable to *G. cf. subinvoluta* Librovitch, in which the umbilicus is 51–52 per cent. of the diameter.

Trilobites

Family PHACOPIDAE Hawle & Corda 1847

Genus PHACOPS Emmrich 1839

Phacops (Phacops) accipitrinus accipitrinus (Phillips 1841)1955 *Phacops (Phacops) accipitrinus accipitrinus* Goldring, p. 46 (with previous synonymy).

Remarks. *P. (Phacops) accipitrinus accipitrinus* occurs commonly in the lower part of the Pilton Beds of north Devon, but it is uncommon in beds of equivalent age in Cornwall.

Although phacopid trilobites occur quite commonly with the rich ammonoid fauna to be found in the siliceous nodules of the Stourscombe Beds, only a single pygidium referable to this species has been recorded. Rare specimens have also been found in the more slaty developments, where they are associated with a rich benthonic fauna. The species has also been collected from the cephalopod limestones of the Lower Petherwin Beds. This represents the oldest horizon from which the fossils have been recorded in this country. However, a comparable range has been observed on the Continent.

Phacops (Phacops) wedekindi Rud. & E. Richter 19261926 *Phacops (Phacops) wedekindi* Rud. & E. Richter, p. 145, pl. 8, figs. 40–43, text-figs. 17c, d.1937 *Phacops (Phacops) wedekindi* Rud. Richter in Schindewolf, p. 39.

Remarks. Specimens referred to this species are identical to those described from Germany but the eyes have fewer (20–25) facets.

Phacops (Cryphops?) ensae Rud. & E. Richter 19261926 *Phacops (Cryphops ?) ensae* Rud. & E. Richter, p. 164, pl. 9, figs. 61–64.1954 *Phacops (Cryphops ?) ensae* Pfeiffer, p. 40, pl. 2, fig. 4.

Remarks. The granulation of the cephalon of specimens from Cornwall is frequently coarser than that described for the species. This is particularly true of the central part of the glabella; towards the periphery, however, the ornament becomes finer and more

closely spaced. In most of the material collected the lateral border of the cephalon is only very weakly ornamented, and in some cases the posterior border appears quite smooth.

Phacops (Cryphops?) wocklumeriae Rud. & E. Richter 1926

1926 *Phacops (Cryphops ?) wocklumeriae* Rud. & E. Richter, p. 167, pl. 9, figs. 65-67.

1937 *Phacops (Cryphops ?) wocklumeriae* Rud. Richter in Schindewolf, p. 39.

1954 *Phacops (Cryphops ?) wocklumeriae* Pfeiffer, p. 41, pl. 2, figs. 5-8.

Remarks. This species, which seems to be limited to the upper part of the Stourscombe Beds, occurs less frequently than *P. (Cryphops ?) ensae*. The tubercles on the testis, particularly on the cheek areas, are more widely spaced and rather coarser than described by Rud. & E. Richter. Whilst the length of the glabella is normally much less than its maximum breadth, one specimen shows a glabella with a length almost equal to its maximum breadth.

Phacops (Dianops) sp.

Plate 29, fig. 4

Remarks. Only a single specimen of a species of the subgenus *P. (Dianops)* has been discovered in Cornwall. The broad outline of the specimen is similar to *P. (Dianops) bartschi* Pfeiffer (1954, p. 46, pl. 2, figs. 6, 7), but it lacks the diagnostic ornament of that species. In addition to the lack of ornament the specimen can be distinguished from *P. (Dianops) griffithides* (Rud. & E. Richter 1919) by the greater breadth of the cephalon and by the more rounded anterior margin of the glabella.

Family PROETIDAE Salter 1864

Genus CHAUNOPROETUS Rud. Richter 1919

Chaunoproetus aff. *carnicus* (Rud. Richter 1913)

Plate 29, figs. 8, 9

1913 *Drevermannia? carnica* Rud. Richter, p. 379, pl. 22, fig. 16.

1926 *Drevermannia? carnica* Rud. & E. Richter, p. 85, pl. 6, figs. ?74, ?75, ?76.

1937 *Drevermannia? (Carnica) carnica* Rud. Richter in Schindewolf, p. 39.

1955 *Drevermannia? (Carnica) carnica* Maksimova, p. 124, pl. 9, figs. ?7, ?8.

Remarks. A single ill-preserved cranidium has been found in the Stourscombe Beds which appears to be reasonably close to the holotype of the species. However, the anterior border is less strongly incurved and the anterior branch of the facial suture diverges more strongly than is normal for the species; the suture is placed closer to the glabella. The occipital ring does not show the large median measurement described by Richter. Glabellar furrow 1p only has been detected.

Specimens figured later by Rud. & E. Richter (1926) show variation particularly in the shape of the glabella and the distance of the facial suture from the glabella. The figures suggest that several species may be involved.

GENUS CYRTOSYMBOLE Rud. Richter 1913

Cyrtosymbole (*Waribole*) aff. *conifera* Rud. & E. Richter 1926

Plate 29, fig. 7

1926 *Cyrtosymbole* (*Waribole*) *conifera* Rud. & E. Richter, p. 53, pl. 3, figs. 37, 38, 40.

Remarks. Several specimens, including an almost complete exoskeleton, from the Stourscombe Beds appear to be very close to this species apart from certain differences in the facial suture. In particular the anterior branch of the suture is more strongly rounded, and cuts the anterior border closer to the median line than in the specimens figured by Rud. & E. Richter. The palpebral lobes are of comparable size to the holotype but are placed a little more anteriorly; γ , and in some cases δ , are farther from the glabella than is usual in the species. The glabella is irregularly, and slightly more strongly, granulated than in the German specimens. No granulation has been observed on the free cheek or pygidium.

Cyrtosymbole (*Waribole*) aff. *italica* (Gortani 1907)

Plate 29, fig. 6

1907 *Dechenella italica* Gortani, p. 39, pl. 1, fig. 27; pl. 2, fig. 32.1912 *Cyrtosymbole* (?) *italica* Rud. Richter, pp. 259, 337.1913 *Cyrtosymbole* (?) *italica* Rud. Richter, p. 398, pl. 23, fig. 2.1913 *Proetus* (*Cyrtosymbole*) *italicus* Gortani, p. 265, text-fig. 1.1926 *Cyrtosymbole* (*Waribole*) *italica* Rud. & E. Richter, p. 51.

Remarks. Several Cornish specimens, although not perfectly preserved, are similar to the species described by Gortani from the Carnic Alps. This species has not been recorded elsewhere, though the closely related *Cyrtosymbole* (*Waribole*) *octofera* Rud. & E. Richter occurs in the *Wocklumeria* Zone in Germany.

The posterior branch of the facial suture, hitherto incompletely figured, diverges moderately strongly from the glabella, reaching the posterior margin a distance from the axial furrow almost equal to half the breadth of the occipital ring. The palpebral lobes are not quite as broad as those figured by Gortani.

A single free cheek has been found which is similar to the incomplete specimen figured by Gortani, but on the cheek area it shows a raised line passing around the anterior part of the eye. This is a similar line to that seen in *C. (Waribole) octofera*, but weaker.

Ornament is not characteristic of the species, but the free cheek described shows a fine granulation and the axial part of the glabella of one cranidium is also granulated.

In the Carnic Alps the species is alleged to occur in the *Clymenia* Zone; however, the clymenid *Postglatziella* is also recorded from the same beds. This is a species generally supposed to be of *Wocklumeria* Zone age. It is thus possible that the Carnic specimens, like those from Cornwall, come from this zone.

Cyrtosymbole (? *Waribole*) *dunhevedensis* Thomas 1909 nom. correct.1909 *Proetus dunhevidensis* Thomas, p. 197, pl. 7, fig. 6.1926 *Cyrtosymbole* (? *Waribole*) *dunhevidensis* Rud. & E. Richter, p. 53.

Remarks. The single specimen of this species located, according to Thomas, in the Southgate Museum, Launceston, has not been found. No further specimens have been found during the present investigation. The spelling of the specific name which, due to a slip in the original description, read *dunhevidensis*, is corrected.

Cyrtosymbole (? *Calybole*) cf. *nepia* Rud. & E. Richter 1926

1926 *Cyrtosymbole nepia* Rud. & E. Richter, p. 61, pl. 4, fig. 50.

1954 *Cyrtosymbole nepia* Pfeiffer, p. 35.

1955 *Cyrtosymbole* (? *Calybole*) *nepia* Maksimova, p. 103, pl. 6, fig. 4.

Remarks. Several minute pygidia have been collected. Although not perfectly preserved these specimens appear to be similar to *C. nepia*, a possible larval form.

Cyrtosymbole (? *Macrobole*) aff. *bergica* Rud. Richter 1913

Plate 29, fig. 5

1913 *Cyrtosymbole bergica* Rud. Richter, p. 387, pl. 22, figs. 22, 23.

1926 *Cyrtosymbole bergica* Rud. Richter, p. 59.

Remarks. An almost complete cephalon, from the Stourscombe Beds, shows closer affinities to the specimen figured by Rud. Richter (1913). However, the exoskeleton where it still remains has a fine granulation which is particularly evident on the free cheeks. Ornament has not previously been described in the species.

The facial suture of the figured specimen, although comparable to the holotype, shows certain differences from it. In particular the posterior branch of the suture which runs parallel, and rather nearer, to the axial furrow than in the German species, cuts the posterior border at a slightly greater distance from the genal angle. γ on the anterior branch is slightly farther from the glabella.

The occipital ring, which is not preserved in the holotype, is comparable to that of *Cyrtosymbole* sp. cf. *bergica* (Rud. & E. Richter 1926, p. 60, pl. 4, figs. 48, 49).

The preservation is such that only the glabellar furrow 1p can be detected.

Pygidia referred to the species show nine clear rings on the axis and three (+1) ribs on the flanks.

This species has not previously been ascribed to any subgenus of *Cyrtosymbole*. The long posterior branch of the facial suture running parallel to the axial furrow suggests that a tentative reference can be made to *C. (Macrobole)*.

Cyrtosymbole (Macrobole) drewerensis Rud. & E. Richter 1951, sens nov.

Plate 29, figs. 14-16

1951 *Cyrtosymbole (Macrobole) drewerensis drewerensis* Rud. & E. Richter, p. 235, pl. 1, figs. 7-11; pl. 5, figs. 47, 48, text-figs. 1M and 3.

1951 *Cyrtosymbole (Macrobole) drewerensis longisuta* Rud. & E. Richter, p. 238, pl. 1, figs. 12, 13; pl. 5, fig. 48.

1954 *Cyrtosymbole (Macrobole) drewerensis longisuta* Pfeiffer, p. 51.

Remarks. This species is the most commonly occurring trilobite in the Yeolmbridge Beds. Variation within the species was noted by Rud. & E. Richter, but it has been

found difficult to refer many of the Cornish specimens to either of the subspecies recognized by them due to the occurrence of intermediate forms and the variation in other characters.

On the whole the palpebral lobes, which are elongate, are broader and the maximum breadth occurs just anterior to glabellar furrow 1p; this is slightly more posterior than is usual in the species. Glabellar furrow 4p is normally developed.

Granulation is varyingly developed and does not appear to be necessarily limited to specimens with *longisuta* type glabellae. For instance, the specimen figured in Pl. 29, figs. 14, 15, is very close in its general form to *C. (Macrobole) drewerensis drewerensis*, but it shows a slight tuberculation at the posterior margin of the glabella. The anterior border of the glabella of this specimen is wider than that figured by Rud. & E. Richter.

Another cranidium (Pl. 29, fig. 16) is very close to *C. (Macrobole) drewerensis longisuta*; the glabella is covered by a fine granulation, but the anterior end of the glabella does not taper so sharply. The palpebral lobes are slightly longer than is usual in the species.

Pygidia referable to this species are not common in the Yeolmbridge Beds. The length of the axis tends to be rather shorter than in the German specimens; in other respects they are closely comparable.

The variation noted in Cornwall in this species with regard to the shape and granulation of the glabella, and in the facial suture, suggests that *C. (Macrobole) drewerensis longisuta* has no taxonomic significance.

Measurements (in mm.)

Specimen	GSM 87099 Pl. 29, figs. 14, 15	GSM 87098 Pl. 29, fig. 16	BU 12897
Length of cranidium	6.5	4.75	5.5
Breadth of cranidium	5.0	2.25	2.75
Length of glabella	5.0	3.25	4.0
Breadth of glabella	4.0	3.0	3.0

Specimen	BU 12905	BU 12904	BU 12902	BU 12901
Length of pygidium	4.0	3.0	6.5	5.5
Breadth of pygidium	7.5	5.5	11.0	10.0
Length of axis	3.0	2.25	5.0	4.5
Breadth of axis	1.75	1.5	2.5	2.75

Cyrtosymbole (Macrobole) duodecimae Rud. & E. Richter 1951

Plate 29, fig. 17

1951 *Cyrtosymbole (Macrobole) duodecimae* Rud. & E. Richter, p. 238, pl. 12, figs. 18–21; pl. 5, fig. 49, text-fig. 4.

1954 *Cyrtosymbole (Macrobole) duodecimae* Pfeiffer, p. 51, pl. 4, fig. 5.

1955 *Cyrtosymbole (Macrobole) duodecimae* Goldring, p. 32, pl. 1, fig. 2, text-figs. 5a, b.

Remarks. Only a few specimens from the Yeolmbridge Beds can be referred to this species and these are very close to the holotype. In the single cranidium the divergence of the facial suture near the posterior border furrow is such that the suture cuts the

posterior margin at a distance from the axial furrow equal to half the breadth of the occipital ring. This distance is greater than that noted by Rud. & E. Richter. The glabella of the Cornish specimen is very slightly more slender than in the holotype. Glabellar furrow 4p has not been observed.

Pygidia are fairly common and agree closely with the described form, but as in the specimens from the Pilton Beds (Goldring 1955) a few show a length of pygidium rather greater than half the breadth.

Measurements (in mm.). GSM 87100 (Pl. 29, fig. 17), length of cranium 4.5; breadth of cranium 3.0; length of glabella 3.25; breadth of glabella 2.7.

Specimen	BU 12911	BU 12912	BU 12913	BU 12914
Length of pygidium	6.0	2.0	3.25	4.0
Breadth of pygidium	10.5	4.0	7.5	9.0
Length of axis	5.0	2.0	2.5	3.0
Breadth of axis	3.5	1.5	2.25	2.5

Cyrtosymbole (Macrobole) aff. blax Rud. & E. Richter 1951

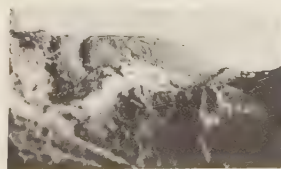
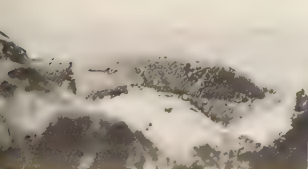
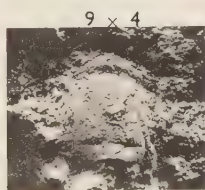
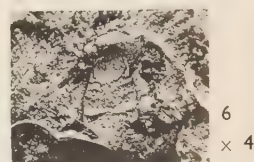
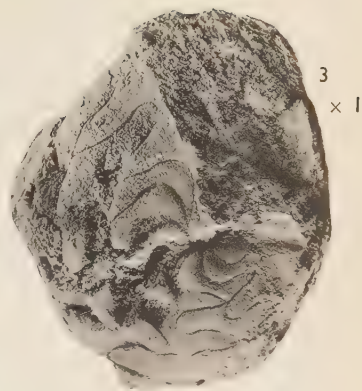
Plate 29, figs. 12, 13

1951 *Cyrtosymbole (Macrobole) blax* Rud. & E. Richter, p. 240, pl. 2, figs. 14–16, ?17; pl. 5, fig. 50, text-fig. 5.

Remarks. A single cranium from the Yeolmbridge Beds is very close to *C. (Macrobole) blax* but shows certain differences from it. The palpebral lobes are broader and placed slightly more posteriorly, the anterior border of the cranium is situated very slightly farther from the glabella, and the granulation of the glabella is only very sparsely distributed.

EXPLANATION OF PLATE 29

- Figs. 1, 2. *Sporadoceras orbiculare* var.; Stourscombe. Lateral and ventral view showing suture-line, GSM 87074, $\times 1$.
- Fig. 3. *Discoclymenia* aff. *cornwallensis* sp. nov. Stourscombe. GSM 87073, $\times 1$.
- Fig. 4. *Phacops (Dianops) sp.*; Stourscombe. Plan view, GSM 87091, $\times 2$.
- Fig. 5. *Cyrtosymbole* (? *Macrobole*) *bergica* Rud. Richter, Overwood Farm, nr. Yeolmbridge. Plan view, GSM 87096, $\times 4$.
- Fig. 6. *Cyrtosymbole (Waribole) aff. italica* (Gortani), Overwood Farm, nr. Yeolmbridge. Plan view, GSM 87094, $\times 4$.
- Fig. 7. *Cyrtosymbole (Waribole) aff. conifera* Rud. & E. Richter, Overwood Farm, nr. Yeolmbridge. Plan view, GSM 87093, $\times 4$.
- Figs. 8, 9. *Chaunoproetus* aff. *carnicus* (Rud. Richter) Stourscombe. Side and plan view, GSM 87092, $\times 4$.
- Figs. 10, 11. *Cyrtosymbole (Macrobole) sp.* Yeolmbridge Slate Quarry. Plan and side view, note elongate glabella, GSM 87097, $\times 4$.
- Figs. 12, 13. *Cyrtosymbole (Macrobole) aff. blax* Rud. & E. Richter, Yeolmbridge Slate Quarry. Plan and side view, GSM 87091, $\times 4$.
- Figs. 14–16. *Cyrtosymbole (Macrobole) drewerensis* Rud. & E. Richter, Yeolmbridge Slate Quarry. 14, 15, Plan and side view of cranium, GSM 87099, $\times 4$. 16, Plan view of cranium, GSM 87098, $\times 4$.
- Fig. 17. *Cyrtosymbole (Macrobole) duodecimae* Rud. & E. Richter, Yeolmbridge Slate Quarry. Plan view, GSM 87100, $\times 4$.



The palpebral lobes are not as large, and the anterior branch of the facial suture diverges more strongly from the glabella at γ , than in the closely related species *C. (Macrobole) mulesi* Goldring (1955).

An incomplete pygidium can probably also be referred to this species. No fine granulation has been detected, and, unlike the pygidium described by Rud. & E. Richter, the anterior portions of the ribs are larger than the posterior. Four ribs can be detected, but only the first two are distinct.

Measurements (in mm.). GSM 87101 (Pl. 29, figs. 12, 13), length of cranidium 6.0; breadth of cranidium 4.5; length of glabella 4.5; breadth of glabella 4.0. BU 12910, length of pygidium 4.0; breadth of pygidium 6.0; length of axis 3.0; breadth of axis 2.0.

Cyrtosymbole (Macrobole) sp.

Plate 29, figs. 10, 11

Description. A species has been noted in the Yeolmbridge Beds which is characterized by a particularly slender cranidium. The glabella is elongate and tapers sharply to the anterior; its length is just over twice its breadth. The preglabellar field is small and the anterior border curved. The occipital furrow is broad and deep, rising posteriorly into the occipital ring which continues the outline of the glabella. At the median line the occipital ring widens slightly and is marked by a mesial tubercle. Four glabellar furrows are present; 1p is a shallow groove curving slightly posteriorly and extending almost to the occipital furrow, 4p is short and indistinct.

The anterior branch of the facial suture diverges moderately from the glabella. β is rounded and lies on a line just posterior to the anterior end of the glabella. The palpebral lobe is small and elongate with γ lying farther from the glabella than δ ; γ is placed between 2p and 3p, δ lies one-third of the distance from 1p to the occipital furrow. The posterior branch of the suture is long and straight and runs parallel to the axial furrow. Near the posterior border it diverges strongly to reach the posterior margin at a distance from the axial furrow equal to half the breadth of the axial ring. The posterior border of the cranidium is much narrower than the occipital ring and only very weakly arched.

Measurements (in mm.). GSM 87097 (Pl. 29, figs. 10, 11), length of cranidium 8.5; breadth of cranidium 4.0; length of glabella 6.25; breadth of glabella 3.0.

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THE MIDDLE PALAEOZOIC SQUAMULATE FAVOSITIDS OF VICTORIA

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ABSTRACT. Of the thirteen nominal species of squamulate favositid described from the Middle Palaeozoic of Eastern Australia and New Zealand, two, *Favosites squamuliferus* Etheridge 1899 and *F. grandiporus* Etheridge 1890, are recognized as discrete species, and one closely related non-squamulate species, *F. moonbiensis* Etheridge 1899, is also recognized. *F. squamuliferus* is interpreted as an extremely variable species containing eight arbitrarily separated formae. Eleven European and Russian species are noted which fall within the range of variation of *F. squamuliferus* and *F. grandiporus*. Favositid wall structure and septal apparatus are also discussed.

INTRODUCTION

THIS study arose during the description of a coral fauna from the basal Devonian (?) Limestones outcropping along the Tyers River, Gippsland, Victoria. As work progressed the squamulate favositids of this fauna were found increasingly difficult to classify in terms of existing Australian 'species' until it was realized that the only satisfactory treatment was to regard them as constituting a single species exhibiting remarkably gross intraspecific variation. Attention was then turned to the favositids occurring in some of the higher Devonian limestone horizons of Victoria, those of the Lilydale Limestone (of upper (?) Lower Devonian age) and of the lower Middle Devonian of Buchan and Bindi. Although the favositids of these horizons have not been investigated in the same detail as those of the Tyers River limestone, the same general conclusion is suggested by the material to hand—that the squamulate favositids show such great variation that satisfactory separation into the previously defined 'species' proves impossible in a moderately large collection.

Intraspecific variation in corals. Very little has been done on the variation of tabulate corals. Jones (1936), in studying the three Silurian species *Favosites gothlandicus* Lamarck, *F. forbesi* E. & H., and *F. multiporus* Lonsdale, considered them to be conspecific and recognized them merely as 'formae' within the species *F. gothlandicus*. Jones considered the variation between the forms to be due solely to environment.

More work has been done on variation in rugose corals. Wells (1937) described in detail variation within the Middle Devonian rugose coral *Heliophyllum halli* E. & H. and in place of eight previously described species recognized the single species with one variety and eleven 'formae' between which there was found to be continuous variation. Wells analysed the possible causes of variation and summarized earlier work on variation in corals. Olliver (1958) described the variation in external form of another Devonian rugose coral *Metriophyllum exiguum* (Billings) and recognized six formae 'which form an intergradational system'.

Certainly more examples of variation have been described in scleractinians, particularly Recent forms. The work of Vaughan (1907) on *Porites compressa*, a living hermatypic coral from Hawaii, should be mentioned. Besides the typical form, Vaughan recognized sixteen formae and four sub-formae between which there is continuous

variation. Further, the difficulty encountered in the definition of species of certain living athermatypic scleractinians is well known. Thus Bernhard (1901) experienced so much difficulty in cataloguing Recent corals in the British Museum (Natural History) that he abandoned the binomial system of nomenclature and substituted a geographical number system.

Nominal species and varieties of squamulate favositids. The following thirteen nominal species and varieties have been proposed for squamulate favositids from various localities from the Lower and Middle Devonian of Eastern Australia and New Zealand:

<i>Favosites grandipora</i> Etheridge 1890.	<i>Alveolites victoriae</i> Chapman 1921.
<i>Favosites squamulifera</i> Etheridge 1899.	<i>Alveolites regularis</i> Chapman 1921.
<i>Cannapora australis</i> Chapman 1908.	<i>Favosites murrumbidgeensis</i> Jones 1937.
<i>Favosites nitida</i> Chapman 1914.	<i>Favosites bryani</i> Jones 1937.
<i>Chaetetes stelliformis</i> Chapman 1918.	<i>Favosites nitidus</i> var. <i>medius</i> Hill and Jones 1940.
<i>Favosites</i> (<i>Emmonsia</i>) <i>spinigera</i> Chapman 1921	<i>Favosites ovatiporus</i> Hill and Jones 1940.
(<i>non</i> Hall 1879).	<i>Favosites pluteus</i> Hill 1950.

To these may also be added *Favosites basaltica* var. *salaebrosa* Etheridge 1899, although Hill (1950) considered that this form does not possess squamulae. However, prior to now, squamulae have not been recognized as such in six of the species listed above.

Of the species which have been proposed, *F. grandiporus* and *F. squamuliferus* are retained while the rest are regarded as synonyms of one or the other, although some of the names have been retained in the description of formae within *F. squamuliferus*. *F. moonbiensis* Etheridge 1899, the non-squamulate counterpart of *F. squamuliferus*, is also regarded as a discrete species, mainly, however, for simplicity of nomenclature.

MORPHOLOGY

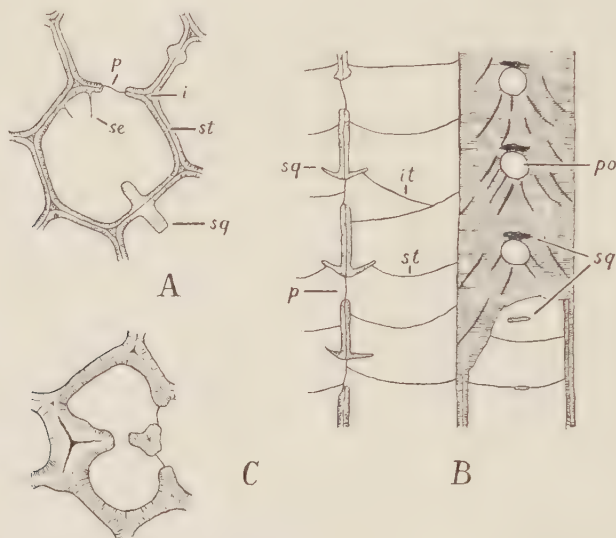
The main factor common to the above species is that they possess comparatively large mural pores usually in a single row toward the centre of each corallite face. Occasionally they may become widely biserial when the corallite face is wide. In most members of the group squamulae are developed above the mural pores, apparently bearing some relation to them. Thus in these characters most members of the group bear resemblance to *Alveolites battersbyi* E. & H., the type species of the genus *Caliapora* Schlüter 1889. Descriptions of the wall structure and septal apparatus of the members of the group are given in some detail as they have considerable bearing on the question of the generic placement of the group as well as on favositid taxonomy generally.

A. *Wall structure.* Swann (1941; 1947) in his description of the *Favosites alpenensis* lineage recognized the presence of calcareous deposits between the corallite walls of certain favositids. The deposits are distinct from the very thin primary walls and peripheral stereozones of the corallites. They are usually differently stained from the calcite of the peripheral stereozones and so are fairly obvious when they occur. Swann (1947) designated these median wall deposits as the 'intramural coenozoone' considering that as such they represented the presence of a coenosarc in favositids.

Deposits between the walls of adjacent corallites in favositids had been noted prior to this. Nicholson (1881, p. 21) in his description of *Favosites inosculans* stated: 'The line of demarcation between the sclerenchyma of any tube and that of its neighbours is in

general recognizable by the presence of a clear linear space. . . . This is well shown in his figures of this species. Etheridge (1899*a*, p. 21) also noted the occurrence of inter-mural deposits towards the corners of the corallites in *F. moonbiensis* and described them as a 'light clear spot in the wall substance'. Lecompte (1936) also noted such deposits and applied the term 'fissure axiale' to them.

Hill (1950) convincingly rejected Swann's idea that intermural deposits were organic structures, for, as Hill comments, the 'coenozone', as described by Swann, does not possess the fibrous structure which is characteristic of all coral material other than the epitheca. Hill suggested that this coenozone was a phenomenon of fossilization caused



TEXT-FIG. 1. Generalized morphology of *F. squamuliferus* and *F. grandiporus* $\times 20$ approx. A, *F. squamuliferus* forma *bryani* based on T.S. 891. Transverse section; Tyers River limestone. B, *F. grandiporus* showing well-developed 'stellate' intermural space with thickening and bleaching of the stereome of the neighbouring corallites in its vicinity. (From T.S. 1209.) Transverse section; Lilydale Limestone. C, *F. squamuliferus* forma *bryani* based on T.S. 917. Longitudinal section; Tyers River limestone. *i*, intermural space; *p*, mural pore with pore plate; *po*, mural pore; *se*, septal spine; *sq*, squamula; *it*, incomplete tabula; *st*, suspended tabula.

by recrystallization along the junction of two sets of fibres. She noted that a similar structure is present along the median line of the septa in specimens of the rugose coral *Pycnactis* from the Silurian of Great Britain.

Ross (1953) substituted the term 'intermural spaces' for Swann's 'intramural coenozone', also considering that Swann's reasons for regarding them organic in origin were unsatisfactory. Ross concluded that, as the spaces were developed between adjacent corallites in particular growth zones, they were produced as a response to adverse environmental conditions.

The author is in agreement with Ross as to the cause of intermural spaces for the same reason (Pl. 34, fig. 3). Furthermore, within the Victorian squamulate favositids they are

to consistently developed that it is hard to imagine them as merely due to fossilization, particularly as other species of *Favosites* occurring side by side with *F. squamuliferus* may not show any development of intermural deposits. In *F. squamuliferus* forma *australis*, a form characterized by subcerioid growth of the corallum, all degrees of development of intermural spaces can be found. In places the corallites are widely separated and elsewhere the walls of adjacent corallites are directly in contact so intermural spaces cannot occur (Pl. 33, fig. 5). Again, with the peculiar 'stellate' intermural spaces discussed below, the stereome of corallites in their immediate vicinity is often bleached and thickened (Pl. 33, figs. 6, 9; Pl. 34, figs. 4, 5; text-fig. 1c). This would be unlikely were intermural deposits merely a fossilization phenomenon.

The intermural spaces of *F. grandiporus* and *F. squamuliferus* and of the closely related non-squamulate *F. moonbiensis* are of a peculiar type. These spaces have already been described by Etheridge (1899a) in the latter species. In this type of intermural space the zone of usually almost clear calcite at the junction of walls of adjacent corallites may appear as a very thin band sometimes enclosing whole corallites (Pl. 33, fig. 12), but more often is more or less confined to the junctions of three or more corallites (Pl. 33, figs. 2, 6-11; text-fig. 1a) although the spaces may irregularly expand elsewhere. When the spaces are confined to the angles of the corallites, they may give rise to 'stellate' structures within the walls (Pl. 33, figs. 6, 9) which may be accentuated by bleaching and thickening of the stereome in their immediate vicinity (Pl. 33, figs. 6, 9; text-fig. 1c). In poorly preserved specimens which have suffered marked recrystallization the 'stellate' structures are often strongly emphasized.

This type of 'stellate' wall structure has been described before in various species of *Favosites*. Swann (1947) noted intermural spaces 'thickening greatest at the corners of the corallites' in *F. warthini*, a species showing strong rounding of the corallites. Similar 'stellate' swellings within the walls at the junctions of corallites have been referred to by various authors, although no explanation has been given as to their nature. Examples are:

Favosites asteriscus Frech (Frech 1899, p. 234), a squamulate species, Middle Devonian, China; *F. proasteriscus* Charlesworth 1914, Lower Devonian, Eastern Alps; *F. stellaris* Chernyshev 1937, Devonian (?), Novaya Zemlya; *F. interstinctus* Regnéll 1941, Siluro-Devonian, Tien-shan. Regnéll also gave a comprehensive survey of 'stellate structures' and described them in *Thamnopora tubifera*.

Porfiriev (1937) appears to have noted the work of Frech who considered that the possession of such stellate swellings within favositid walls could be regarded as having generic significance. Porfiriev proposed the genus *Asteriophyllum* based on *A. enigmatium*, a species differing only in this respect from *Favosites*.

As 'stellate swellings' appear to be caused by the pulling apart of the walls of adjacent corallites particularly at their corners and the thickening of the stereoplasm of the corallites in their vicinity and were probably developed due to adverse environmental conditions, it is doubtful whether their possession should be regarded as being of generic significance in favositids. Naturally, when cylindrical corallites are packed into a cerioid growth habit, the walls at the corners are not so closely in contact as elsewhere (Pl. 33, fig. 5). Some species exhibit this more than others. For this reason the genus *Asteriophyllum* is best regarded as a synonym of *Favosites*.

Even greater taxonomic importance has been placed on the presence of intermural

spaces in favositids. Recently Lafuste (1958, p. 412), on the basis of Swann's (1941) description of favositid wall structure, states of his separation of *Thecia* E. & H. from the Favositidae: 'It is convenient to set apart from *Thecia* the forms which possess a wall of the kind which Swann described in *Favosites*, i.e., a median lamella, two thin dark planes on each side, and two borders of perpendicular fibres. Such a microstructure disagrees with the trabecular constitution of *Thecia* chiefly by its continuity along the periphery of the corallites. . . . It is therefore impossible to agree with Hill and Stumm, who put *Thecia* in the family Favositidae.' Thus even family significance has been placed on a character which at the best can be regarded as being developed as a response to environment.

B. Septal apparatus. (i) *Septal spines.* The septal apparatus of *F. squamuliferus* is one of the most variable characters of a particularly variable species. Thin discrete septal spines may occur together with squamulae (Pl. 33, figs. 1, 3; text-fig. 1A). The septal spines are remarkably sporadic in their occurrence and are often present only in certain parts of a corallum. Their presence or absence bears little or no relationship with the various formae of *F. squamuliferus* and they have no correlation with the stratigraphic occurrence of the species. That they have not been observed in certain specimens could well be due to poor preservation, but this cannot be argued for most of the material examined. They are apparently absent in some of the formae of *F. squamuliferus*, but this is most likely due to the small number of specimens so far examined belonging to those formae.

(ii) *Squamulae.* The term 'squamula' as used here implies merely a horizontal or flattened, usually blunt septal spine (see text-fig. 1). There can be no doubt that squamulae represent modified septal spines. The view of earlier authors (e.g. Nicholson 1879; Smith and Gullich 1925; Jones 1936; Weissmermel 1939) that squamulae were a form of 'degenerate' tabulae appears to have been based partly on a misconception as to their nature. Nicholson, for example, considered what are undoubtedly broken tabulae to be squamulae in *F. forbesi*. Swann gave the following observations in support of the septal nature of squamulae: 1, Squamulae, in common with septal spines, are continuous with peripheral stereozones of corallites. 2, Squamulae are arranged in vertical rows similar to septal spines. 3, Squamulae were apparently secreted by the polyp well up from the basal disc. Swann did not mention the trabeculate nature of squamulae which had been earlier established by Kraicz (1937) in *F. hemisphaericus* var. *bohemicus* Počta. It has also been discussed by Hill (1950) in describing some Australian favositids.

Although squamulae had been recognized by Etheridge (1899a) in his description of *F. squamuliferus* they had not been recorded as such in any of the other closely related nominal species till Hill (1950) drew attention to their occurrence in *F. stelliformis* (Chapman), *F. bryani* Jones, and *F. murrumbidgeensis* Jones, as well as in a new species *F. pluteus*. Hill distinguished two types of squamulae—'eaves-like' squamulae which occur in the first four of the above species, and 'shelf-type' squamulae typical of *F. pluteus*. The 'eaves-like' squamulae occur back-to-back in adjacent corallites above each mural pore, as they are developed from the fibrous stereome of the upper margin. They are generally upwardly directed and thicken toward their base. The 'shelf-type' squamulae, on the other hand, consist of horizontal plate-like projections of uniform thickness often bearing no relation to the mural pores and so not developed back to back on opposite sides of the walls.

An examination of a collection of specimens from various localities in Victoria in addition to the large collections from the Tyers River limestone suggests that this distinction cannot be maintained. The shape of squamulae and their relation to the mural pores is extremely variable even in different parts of the one corallum. Even a specimen illustrated as *F. pluteus* by Hill (1949, pl. 8, fig. 26a, b; M.U.G.D.T.S. 649) shows 'shelf' squamulae occurring side by side with 'eaves' squamulae. In this slide the uniform thickness of many of the squamulae is apparently due to the deposition of an uneven layer of secondary calcite (Pl. 31, fig. 5). Further, in some specimens upwardly directed tapering squamulae may bear no relation to the mural pores (Pl. 31, fig. 1) while in still others thin flat squamulae may occur back to back in adjacent corallites (Pl. 31, figs. 6, 8). There is perhaps a trend for the squamulae to lose their relationship with the mural pores and become longer and thinner, as forms showing squamulae of this type are more common in the Middle Devonian of Buchan and Bindi than at the base of the Devonian. Confirmation of this would lie in a detailed examination of our Middle Devonian favositids. It should be pointed out that Hill (1954) was unable to uphold the separation of *F. pluteus* from *F. bryani* in her description of the coral fauna from Waratah Bay.

One specimen showed a further variation in the squamulae. T.S. 892 (Pl. 31, figs. 1, 2) shows the cross-sections of the cut ends of the squamulae where the section passes close to the plane of the corallite wall. In places this section of the squamulae can be seen to be circular, and so they may be regarded as discrete septal spines. It can be seen also that this is not consistent even within the one section; in other places they are flattened in cross-section.

The degree of development of squamulae can be seen to have been related to the rate of growth of the corallum. In zones where the tabulae are closely spaced (i.e. apparently zones of slow growth) the squamulae are usually strong and moderately closely spaced; in zones of rapid growth with distant tabulae the squamulae may be reduced so as to appear absent in parts of the corallum (Pl. 30, fig. 3). The 'species' *F. ovatiflorus* Hill and Jones 1940 is based on a corallum showing well-spaced tabulae and a virtual absence of squamulae, together with large, ovate mural pores (Pl. 32, figs. 1, 2) the shape of which again appears to be a function of the rapid growth of the corallum. This, in fact, can be seen in the one section; portions of T.S. 913 and T.S. 1031 (Pl. 34, fig. 1) show well-spaced tabulae and large ovate mural pores and reduced squamulae while other zones of the coralla have the appearance of *F. nitidus* with closely spaced tabulae, moderately strong squamulae, and comparatively small mural pores. The variable development of squamulae can be pointed to in *F. grandiporus* also. This species has typically a sub-digitate corallum with a rapidly grown axial zone and a more slowly grown distal region. In the axial part of the corallum the squamulae are small and slender, whereas distally they are thick and large (Pl. 32, figs. 6, 7).

The taxonomic importance of the presence of squamulae should also be discussed. Hill (1950) with reservation placed the species *F. moonbiensis* Etheridge in the synonymy of *F. bryani* (here regarded as a forma of *F. squamuliferus*) as she noted the two were indistinguishable except that *F. bryani* possessed squamulae. If the two species are not very closely related then we have here a remarkable case of virtually isochronous parallelism, particularly in view of the fact that both possess intermural deposits confined to the corallite corners (cf. Pl. 31, fig. 3 and Pl. 33, fig. 2 with Pl. 31, figs. 2, 4, 7 and Pl. 33,

fig. 3). Extensive collecting from the limestones and underlying mudstones along the Tyers River showed that *F. moonbiensis* is one of the most common favositids of the mudstone facies, whereas it is completely absent in the overlying limestones. On the other hand, the various formae of *F. squamuliferus* are confined to the limestone facies except for two isolated coralla collected in the upper, more calcareous phases of the mudstone. (For further details of the distribution of these species see Philip 1960.) The few other localities in Eastern Australia from which *F. moonbiensis* has been recorded should be investigated to find whether this facies relationship exists elsewhere. This relationship between *F. squamuliferus* and *F. moonbiensis* suggests that squamulae in the Victorian forms were developed as a response to gross environmental changes. This view is perhaps supported by the fact that in longitudinal sections of *F. moonbiensis* swellings in the stereome of the walls above the mural pores are sometimes encountered. These could well represent 'incipient' squamulae (Pl. 31, fig. 3).

This whole discussion raises the question of the relationship of *Favosites* to *Caliapora*. Schlüter and Emmonsia E. & H. Hill and Stumm (1956, p. F464) define *Caliapora* to include forms 'like *Emmonsia* but with squamulae with concave upper surfaces'. As has been already stated and is obvious in an examination of the plates, the group dealt with here exhibits such extreme variation in the shape of squamulae that even specific significance cannot be placed on this feature. It seems then that *Caliapora* cannot be separated from *Emmonsia*. Schouppé (1951; 1954a) has continued to regard *Caliapora* as a subgenus of *Alveolites*. There appears to be certain justification in regarding *Caliapora*-like forms as being related to *Alveolites* for certain species (e.g. *Alveolites fornicatus* Schlüter) usually placed in that genus are very similar morphologically to the type species of *Caliapora*.

None of the more recent authors who have upheld the generic status of *Emmonsia* has doubted the polyphyletic origin of species placed in this group. Smith and Gullic (1925) explicitly stated that the genus is polyphyletic, 'an assembly of polygerontic forms exhibiting a form of degeneration common in many lineages of *Favosites*'. This view is again expressed by Fenton and Fenton (1936), Swann (1947), and Stumm (1949). Great difficulty has been encountered in the application of the genus. Fenton and Fenton (1936, p. 22) would retain '*Favosites* for forms in which $\frac{2}{3}$ of the tabular structures are complete (tabulae) and introduce *Emmonsia* when squamulae number more than $\frac{1}{3}$ the total . . .', a procedure which appears arbitrary in the extreme. Ross (1953) overcame the difficulty of the polyphyletic origin of the genus by employing *Emmonsia* as a genomorph of *Favosites* in the sense in which the concept was introduced (Smith and Lang 1930) for a morphological stage which occurs in different lineages. In dealing with the present group of favositids it is doubtful whether even this procedure is justified, as the squamulae here were apparently developed as a response to gross environmental changes.

It should be noted that Swann (1947) suggested as a new generic character of *Emmonsia* the alternation of squamulae with mural pores, but Ross (1953) has shown (as also did Swann) that this character is developed in different lineages of the North American favositids.

The present conclusion, then, is that *Caliapora* Schlüter and *Emmonsia* E. & H. are best regarded as synonyms of *Favosites*, and the application of *Emmonsia* as a genomorph is not justified in dealing with the Eastern Australian Devonian favositids.

F. grandiporus Etheridge possesses a subdigitate corallum and also shows considerable distal thickening of the corallite walls (Pl. 32, figs. 6, 7). In these characters it approaches species which are generally referred to *Thamnopora*. Swann noted a similar case in his description of *F. alpenensis* lineage. One offshoot from the main lineage, *F. dumosus* Winchell, possesses the same distal thickening and growth habit as *Thamnopora*. This again suggests a possible polyphyletic origin of species included in *Thamnopora*.

The Upper Carboniferous North American genus *Acaciapora* Moore and Jeffords 1945 differs from *Thamnopora* only in the possession of squamulae. Out of the context of its relationship with *F. squamuliferus*, *F. grandiporus* could be placed in this genus, if separation of this genus were considered justified.

METHOD OF STUDY

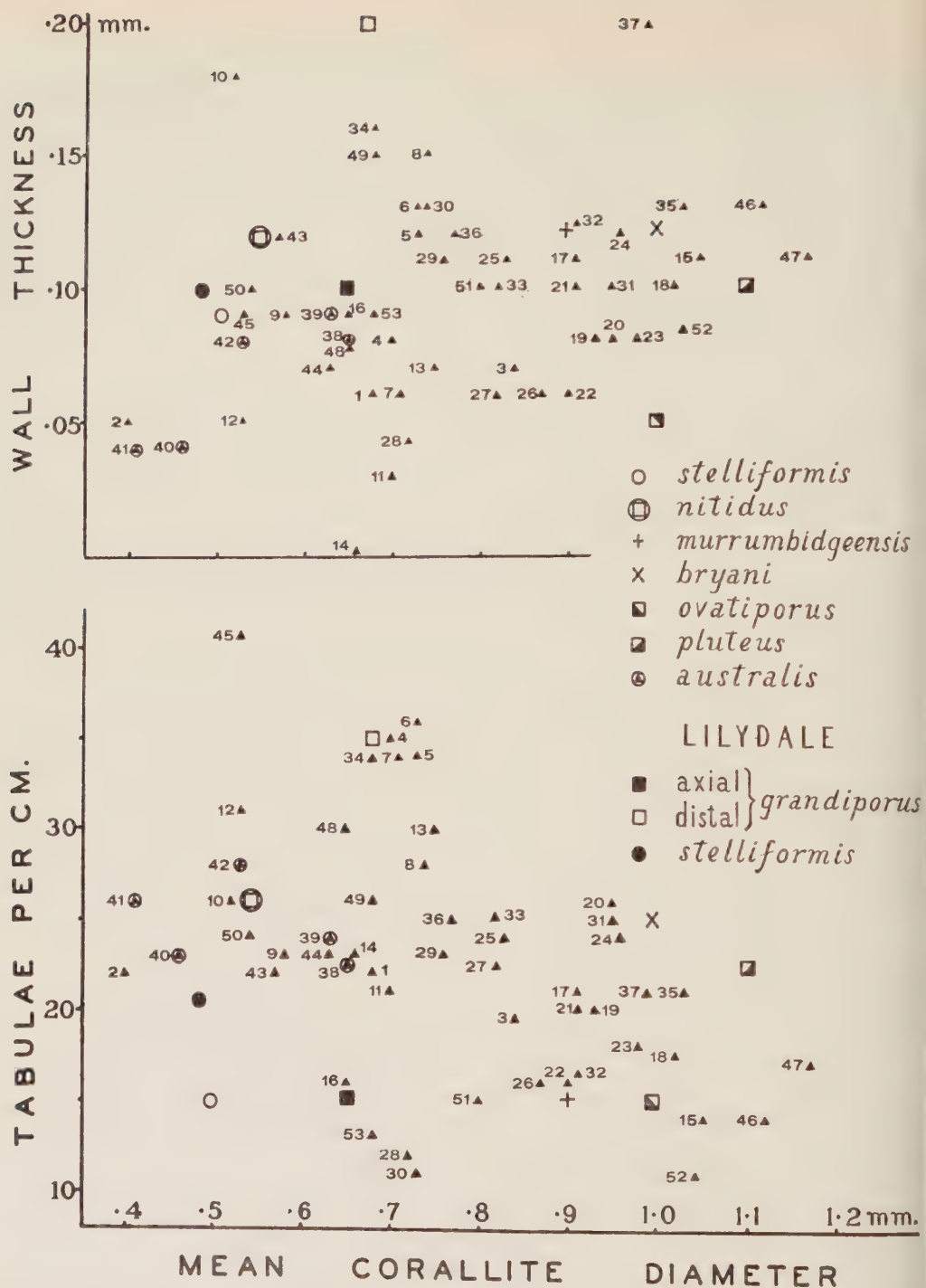
The fauna investigated in detail was taken from the limestone horizon exposed in the valley of the southern part of the Tyers River, Gippsland, Victoria. Precise correlation of this fauna with overseas sections is difficult, but it is best regarded as being of basal Devonian age. Coralla were collected from various localities in the limestone which reaches a maximum thickness of less than 200 feet. In view of the fact that *F. squamuliferus* is a long-ranging species (from Upper Silurian to Middle Devonian) the coralla were treated as being contemporaneous. This is further justified by the fact that there is no faunal differentiation within the limestone horizon apart from that which can be ascribed to facies changes.

In the early stages of the work, when only a few coralla had been examined, many of the squamulate 'species' listed earlier were recognized in the fauna, but as more and more specimens were examined separation into the previously defined 'species' became wellnigh impossible. Differentiation of these 'species' has proved troublesome before, even in small collections (Hill 1954).

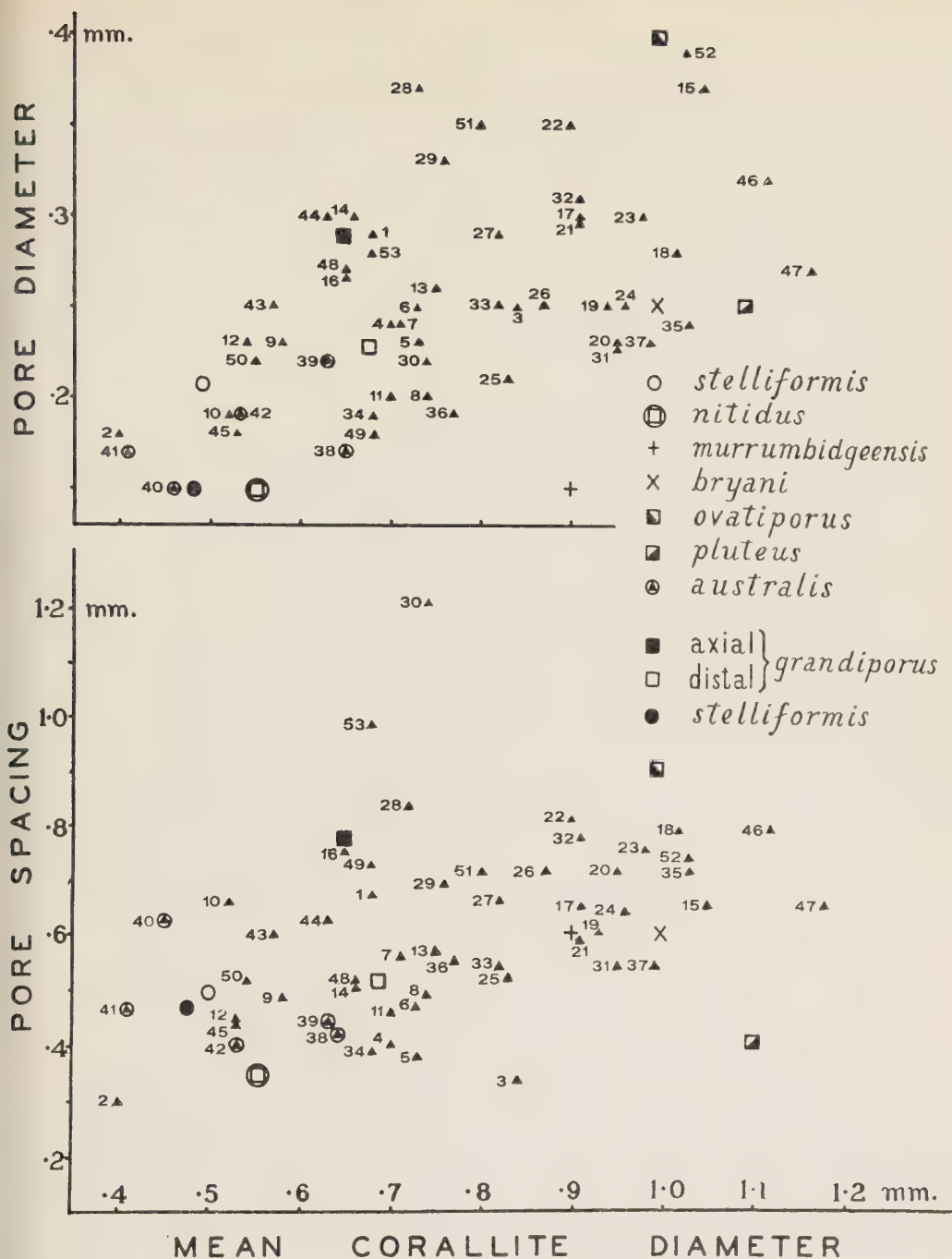
It was found that the only adequate way to characterize the extreme variation of the squamulate favositids within the Tyers fauna, short of illustration of virtually each specimen, was to construct scatter diagrams of the various commensurable characters by which favositid species are defined. A few particularly variable coralla were rejected as it was considered that they could not be defined adequately merely by average measurements.

Of the 135 coralla collected, 53 were considered suitable, after the preparation of sections, for the calculation of average measurements. The features determined were:

1. *Mean corallite diameter.* An endeavour was made to measure the maximum diameter of the corallites in thin sections normal to the direction of growth. The diameter was measured from the boundary of the primary walls of the corallites. At times this measurement was made with polished surfaces.
2. *Mean number of tabulae per centimetre.* The number of tabulae over a comparatively large length of corallites was measured to include the different spacing of tabulae within the one corallum. At least 10 cm. of corallite length was measured for each corallum, and usually the figure was greatly in excess of this.
3. *Mean diameter of mural pores.* The diameter of all mural pores visible in each section was taken. In one case this was as few as six, but usually many more were used. As the mural pores were often oval, the square root of the height by the width was taken as the diameter.
4. *Average spacing of mural pores.* This measurement is the vertical spacing of the centres of mural pores and was arrived at by the addition of half the vertical diameter of two consecutive mural pores and the length of corallite between them. Measurements 3 and 4 were made simultaneously although



TEXT-FIG. 2. Scatter diagrams of the average wall thickness and average number of tabulae per centimetre against the mean corallite diameter for fifty-three specimens of *F. squamuliferus* from the Tyers River limestone. Superimposed are the approximate positions of six of the more commonly used 'species' of squamulate favositid, the positions of which were arrived at from the descriptions and figures of various authors. Specimens of *F. squamuliferus* forma *australis* from the Tyers River limestone are designated by a different symbol. The two illustrated specimens from the Lilydale Limestone are also included. No morphological separation of the fauna into 'species' is possible.



EXT-FIG. 3. Scatter diagrams of average mural pore diameter and average mural pore spacing against mean corallite diameter for fifty-three specimens of *F. squamuliferus* from the Tyers River limestone. Superimposed are the approximate positions of the more commonly used 'species' of squamulate favosites, which were arrived at from the descriptions and figures of various authors. Specimens of *F. squamuliferus* forma *australis* from the Tyers River limestone are designated by a different symbol. The two illustrated specimens from the Lilydale Limestone are also included. Only an arbitrary separation is possible.

the spacing of the pores was measured also in well-oriented longitudinal sections normal to the corallite faces where the pores are represented by breaks in the walls.

5. *Mean diameter of corallite walls.* This included the total diameter of the walls of two adjacent corallites and in places included intermural spaces. It was measured half-way between the corners of the corallites so as to avoid measurements through the thickened corners in specimens where the corallites were rounded.

An attempt was also made to characterize the orientation and length of the squamulae, but these proved so variable even in the one corallum that this was abandoned.

The thin sections used in the construction of the scatter diagrams are in Melbourne University Geology Department Thin Section Collection T.S. 849 and 861 to 965 inclusive. The average characters arrived at for each of the fifty-three specimens are entered in the thin-section catalogue.

Examination of the four scatter diagrams reproduced here shows that it is impossible to subdivide morphologically this fauna into components between which there is no intergradation. The same is also true of the six other possible scatter diagrams which were constructed. Certain individual specimens may appear to be isolated from the group in one particular character (14, 37—wall thickness; 30—pore spacing; 45—tabulae spacing), but these individuals represent the extreme development of a feature already shown to a lesser degree by other members of the group. The divergent types are represented as formae within the single species.

The scatter diagrams show a certain degree of correlation between morphological features which could be expected on general grounds. For example, with increasing corallite diameter the mural pores generally become larger and more distant while the wall thickness perhaps tends to increase. Another trend which can be seen from the scatter diagrams which are not reproduced here is an increase of the spacing of the mural pores with increase in spacing of the tabulae. Overall, however, it can be seen that there is no great degree of correlation between the various morphological features.

SYSTEMATIC DESCRIPTIONS

Genus FAVOSITES Lamarck

Favosites grandiporus Etheridge

Plate 32, figs. 6, 7; Plate 33, fig. 9; Plate 34, fig. 4; text-fig. 1c

Favosites grandipora Etheridge 1890, p. 61, 2, pl. 8, figs. 6–9.

Alveolites victoriae Chapman 1921, p. 215, pl. 11, figs. 17, 18.

Diagnosis. Corallum subdigitate, cylindrical, sometimes amalgamated by later overgrowths. Corallites gently expanding in axial region, bending sharply to emerge normal to the surface of the corallum; corallites polygonal in axial region, usually rounded distally, diameter averaging between 0.6 and 1 mm.; distally the mural pores are more closely spaced and smaller, the tabulae more crowded, the walls thicker, and the squamulae more strongly developed.

Observations. The measurements of a typical specimen can be seen in text-figs. 2, 3. It may be that this species, differing from *F. squamuliferus* in the growth habit and distal thickening of the corallites, is transitional morphologically with that species. However, the material so far investigated from the Lilydale Limestone, the only horizon from

which *F. grandiporus* is known, suggests that it is a separable species. Distal thickening of corallites in tabulate corals is generally regarded as a character of generic merit.

Reference to Chapman's type slides of *Alveolites victoriae* shows that this species is based on a specimen of *F. grandiporus* with comparatively large corallites. In his original description Chapman noted the distal thickening of the walls of the corallites and his plate shows the characteristic wall structure of *F. grandiporus*. Chapman apparently regarded as 'teeth' the remnants of the walls of corallites on each side of a mural pore, as encountered in transverse sections, and so placed the species in the genus *Alveolites*.

Of the well-developed squamulae in this species Jones (1937, p. 93) has stated: 'The appearance of spines in longitudinal section is caused by the breaking down of the wall where the large mural pores almost meet.'

Favosites squamuliferus Etheridge

Favosites squamulifera Etheridge 1899a, pp. 166-7, pl. 38, figs. 4, 5.

Emmonsia squamulifera (Etheridge fil.); Jones 1937, p. 99.

Diagnosis (after Etheridge). Corallum massive, corallites approximately the same size, averaging 1 mm. or less in diameter, mural pores small, in a single column on each corallite face; squamulae horizontal or inclined, tabulae moderately closely spaced.

Observations. Etheridge's meagre description and inadequate figures make the interpretation of this species difficult. The type specimens are reported by Hill (1950) to be missing, and there is even some doubt as to the type locality of the species. Not until the tabulate corals of the Tamworth district of New South Wales are investigated in detail will this species be properly understood. Because of this the use of the species here is undesirable, but as it cannot be questioned that it is the first name employed in the literature to this species it is retained.

It is more than likely that *F. squamuliferus* will prove to be identical with *F. bryani* Jones. As *F. bryani* is much more precisely defined, it is retained in the naming of the forma which most probably includes *F. squamuliferus* s.s.

Favosites squamuliferus forma *bryani* Jones (forma α^1)

Plate 31, figs. 1, 2, 4-6, 8; Plate 33, fig. 3; text-fig. 1A, B

?*Favosites squamulifera* Etheridge 1899a, pp. 166-7, pl. 38, figs. 4, 5.

?*Favosites gothlandica* Lamarck; Chapman 1920, p. 186 (*partim*), pl. 23, figs. 18, 19.

Favosites (*Emmonsia*) *spinigera* Chapman 1921, pp. 214-15, pl. 9, fig. 21 (*non* Hall 1879, p. 108, pl. 4, figs. 1-5).

Favosites murrumbidgeensis Jones M. S., in Allan 1935, p. 7, pl. 4, figs. 5, 6.

¹ The formae recognized within *F. squamuliferus* are designated with a Greek letter, a procedure used by Olliver (1958). Although the 'forma', as used by various authors, has no standing as a taxonomic category and so the laws of priority do not apply, later authors are liable to elevate the names employed as formae to the rank of subspecies. Thus Bassler (1950, p. 81) lists Lecompte's (1939) two formae of *F. goldfussi*, *F. goldfussi* forma *regularis*, and *F. goldfussi* forma *pyriformis* as subspecies, thus presumably making the former a further homonym of *Favosites regularis* (Chapman 1920) along with *F. kennihoensis* var. *regularis* Ozaki 1934, *F. regularis* Jones 1937, and *F. hisingeri* var. *regularis* Ruzhkin 1938 and the latter a homonym of *F. pyriformis* (Hall 1852). To avoid such possible contingencies it is best to refrain from applying to new formae names which could be used as trivial appellations.

Favosites bryani Jones 1937, pp. 96–97, pl. 15, figs. 3–6.

Favosites murrumbidgeensis Jones 1937, p. 98, pl. 16, figs. 5, 6.

?*Emmonsia squamulifera* (Eth. fil.); Jones 1937, p. 99.

Favosites bryani Jones; Hill and Jones 1940, pp. 190–1, pl. 5, figs. 2a, b; Jones 1941, p. 42, pl. 1, fig. 1; Hill 1942, p. 8, pl. 2, fig. 6; Jones 1944, p. 34, pl. 1, figs. 1, 2; Hill 1950, p. 150, pl. 7, figs. 23, 24.

Favosites pluteus Hill 1950, p. 151, pl. 8, figs. 25–26.

Favosites affn. *bryani* Jones; Hill 1954, pp. 113–14, pl. 9, figs. 23, 24.

Material. Specimens 3, 17–21, 23–27, 31–33, 35, 46, 47; figured slides T.S. 891 (18); T.S. 892 (20); T.S. 895 (21); T.S. 917 (31); T.S. 921 (32) and T.S. 649 from Rocky Camp, Murrindal Limestone, Buchan.

Diagnosis. Corallum massive, corallites polyhedral averaging greater than 0.8 mm. diameter and usually less than 1.5 mm.; mural pores uniserial circular to slightly ovate between 0.15 and 0.35 mm. in diameter and between 0.3 and 0.8 mm. apart. Squamulae

EXPLANATION OF PLATE 30

Longitudinal sections; all figures $\times 10$ and unretouched. The serial number in parentheses refers to the number of the specimen in the scatter diagrams, and the prefix 'T.S.' refers to catalogue numbers in the Melbourne University Geology Department Thin Section Collection of Fossils.

Figs. 1, 2. *Favosites squamuliferus* forma *stelliformis* (γ). 1, T.S. 849 (2). Small corallite diameter, poorly developed squamulae, and well-spaced tabulae developed in places at similar heights in adjacent corallites. Tyers River limestone. 2, T.S. 1211 (also Pl. 33, fig. 6). Well-developed flattened squamulae occurring back to back in neighbouring corallites above mural pores. 'Pore plates' usually present in *F. squamuliferus*, also seen. Lilydale Limestone.

Figs. 3–5, 7. *F. squamuliferus* forma *nitidus* (β). 3, T.S. 875 (9) (also Pl. 33, fig. 7). Variable development of squamulae. 4, T.S. 924 (34) (also Pl. 33, fig. 8). Very closely spaced suspended and 'incomplete' tabulae and thick-based squamulae. 5, T.S. 880 (12). Moderately large mural pores and small squamulae. 7, T.S. 865 (4). Mural pores and small squamulae. All from Tyers River limestone.

Fig. 6. *F. squamuliferus* forma *australis* (δ). T.S. 935 (39) (also Pl. 33, fig. 5). Wide, irregular inter-mural spaces, well-spaced tabulae, and small squamulae. Tyers River limestone.

Fig. 8. *F. squamuliferus* forma η . T.S. 882 (14) (also Pl. 33, fig. 4). Extremely thin-walled form with small squamulae and well-spaced tabulae. Mural pores also seen. Tyers River limestone.

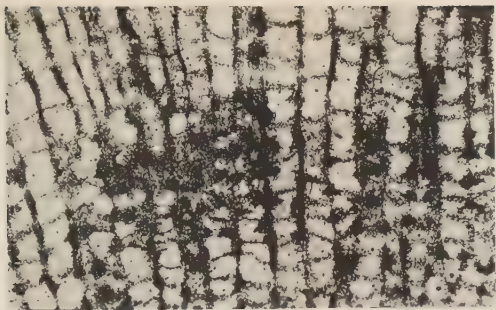
EXPLANATION OF PLATE 31

Longitudinal sections; all figures $\times 10$ and unretouched.

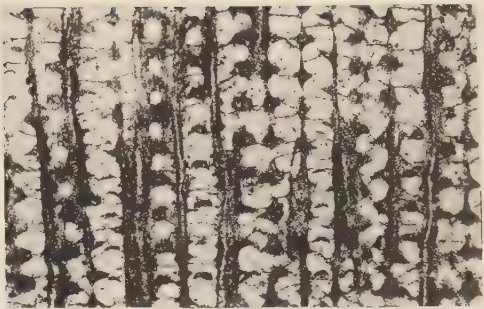
Figs. 1, 2, 4–6, 8. *F. squamuliferus* forma *bryani* (α). 1, 2, T.S. 892 (20). Strong, upwardly curved squamulae, in places not occurring back to back in adjacent corallites. The cut ends of the squamulae are in places circular rather than flattened. Tyers River limestone. 4, T.S. 917 (31). Short, upwardly directed squamulae, well-spaced tabulae, and a single column of moderately large mural pores. Tyers River limestone. 5, T.S. 649. Slide illustrated as '*F. pluteus*' (Hill 1950, pl. 18, figs. 26a, b). Note upwardly directed, tapering squamulae above the mural pores. An irregular deposit of secondary calcite can be seen obscuring the taper of the squamulae and giving also the appearance of very thick tabulae. Murrindal Limestone, Rocky Camp, Buchan. 6, T.S. 921 (32). Similar specimen with horizontally directed squamulae, some of which do not occur back to back in neighbouring corallites. Tyers River limestone. 8, T.S. 895 (21). Large, closely spaced mural pores, and thin, delicate squamulae, thus approaching forma *ovatiporus*. Tyers River limestone.

Fig. 3. *F. moonbiensis* Etheridge. T.S. 800 (also Pl. 33, fig. 2), cf. figs. 4, 7. Note similarity between this form and *F. squamuliferus* forma *bryani*. Occasional swellings in the stereome of the walls above mural pores may be encountered (e.g. top right-hand corner of figure). These swellings could represent 'incipient' squamulae. Mudstone beneath the limestone, Tyers River.

Fig. 7. *F. squamuliferus* forma ζ . T.S. 915 (30). Note the small, distantly spaced mural pores, well-separated tabulae, and reduced squamulae. Tyers River limestone.



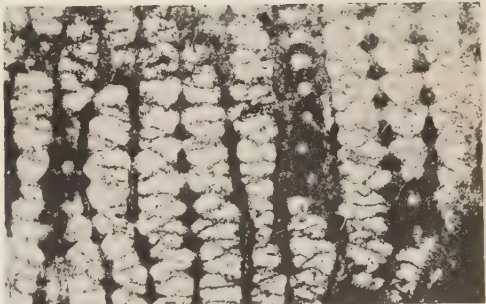
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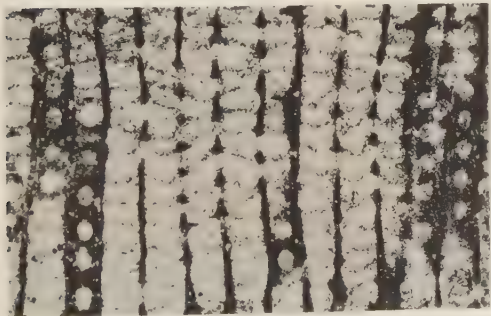
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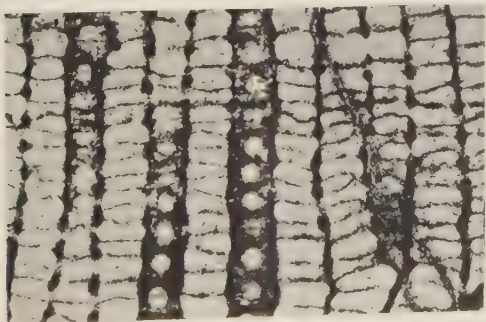
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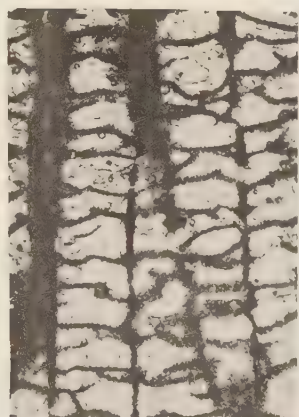
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highly variable, horizontal or upwardly directed, developed either back to back in adjacent corallites above the mural pores or isolated. Slender septal spines may also be present.

Observations. *F. squamuliferus* forma *bryani* is arbitrarily separated from forma *nitidus* (β) and forma *stelliformis* (γ) by the corallite diameter. In the forms with smaller corallite diameter the tabulae may be more closely spaced. As can be seen from the synonymy of this species five different specific names have been applied to this forma.

F. squamuliferus forma *nitidus* (β)

Plate 30, figs. 3–5, 7; Plate 34, figs. 1, 7, 8, 10

?*Favosites* sp. indet. Etheridge 1899*b*, p. 33, pl. B, figs. 7–9.

Favosites nitida Chapman 1914, p. 309, pl. 54, figs. 21–23; pl. 55, figs. 24, 25.

Favosites forbesi (partim) Chapman 1914, pl. 53, fig. 19 (*non*. pl. 56, fig. 27).

Favosites nitida Chapman; Jones 1937, p. 93, pl. 12, figs. 4, 5.

Favosites nitidus Chapman; Hill and Jones 1940, p. 198, pl. 6, figs. 3*a*–*c*.

Favosites nitidus var. *medius* Hill and Jones 1940, pp. 198–9, pl. 6, figs. 4*a*, *b*; pl. 7, figs. 1*a*, *b*, 2.

Favosites nitidus Chapman; Jones 1941, p. 43, pl. 1, fig. 2; Hill 1950, pp. 148–9, pl. 7, figs. 20*a*, *b*;
Hill 1954, p. 113, pl. 9, figs. 25*a*, *b*.

Material. Specimens 1, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 16, 29, 34, 44, 45, 48, 50, 53; figured slides T.S. 865(4); T.S. 870(6); T.S. 875–6(9); T.S. 880(12); T.S. 924–5(34); T.S. 967; T.S. 1031.

Diagnosis. *F. squamuliferus* with average corallite diameter between 0.5 and 0.8 mm.

Observations. In general, besides the smaller corallite diameter, this forma has smaller mural pores and may also have closer tabulae than is usual in forma *bryani*.

Hill and Jones (1940) note that there is a complete gradation between *F. nitidus* and *F. salaebrosus* Etheridge 1899 and that *F. salaebrosus* should be set aside for forms having a considerable number of reclined corallites which as a result appear alveolitoid in transverse sections. They proposed *F. nitidus* var. *medius* to include forms intermediate between *F. nitidus* and *F. salaebrosus*. If squamulae prove to be present in the type slides of *F. salaebrosus* then this species could be set aside as a further forma of *F. squamuliferus* to include forms with reclined corallites.

F. squamuliferus forma *stelliformis* Chapman (γ)

Plate 30, figs. 1, 3; Plate 33, fig. 6

Chaetetes stelliformis Chapman 1918, p. 393, pl. 42, figs. 1–3.

Alveolites regularis Chapman 1920, p. 216, pl. 11, figs. 19, 20.

Favosites stelliformis (Chapman); Hill, 1950, p. 149, pl. 7, figs. 21, 22.

Material. Specimen 2; figured slides T.S. 849 (2) also T.S. 1210-1 from the Lilydale Limestone.

Diagnosis. *F. squamuliferus* with the average diameter of corallites less than 0.5 mm.

Observations. Hill (1950, p. 149), although recognizing the relationship to *F. squamuliferus* forma *nitidus*, suggested by this form from Buchan, states: 'Its unusual characters, the numerous oval pores separated by squamular aggregations of trabeculae and the regular tabular floors throughout the corallum, suggest it might be wise to erect a new genus for it.' The similar height of tabulae in adjacent corallites is fairly common in *F. squamuliferus*, particularly in those specimens with small corallites. The holotype of *F. nitidus* var. *medius* (Hill and Jones 1940, pl. 6, fig. 4*a*) shows this character although

perhaps not as strikingly as in the specimens illustrated as *F. stelliformis* by Hill. It should be noted that Chapman's original figures of *F. stelliformis* do not show this at all well, nor do other specimens of this forma from Buchan and Bindi.

F. squamuliferus forma *australis* (Chapman) (δ)

Plate 30, fig. 6; Plate 33, fig. 5; Plate 34, fig. 3

Cannapora australis Chapman 1907, p. 76, pl. 3, figs. 6, 7; pl. 8, figs. 17, 18.

Material. Specimens 38–42; figured slides T.S. 934–5 (39); T.S. 985.

Diagnosis. *F. squamuliferus* with small corallite diameter and sub-ceriod growth allowing separation of the corallites.

Observations. Chapman's type specimens of this species were collected from the Tyers River limestone, but have apparently been lost. The topotype illustrated matches Chapman's figures very closely. Although the corallites may not all be in contact in other formae of this species (a feature which is often difficult to detect even in thin section) extreme cases of this feature appear to be confined to specimens of *F. squamuliferus* with small corallite diameter, well-spaced tabulae, and reduced squamulae.

F. squamuliferus forma *ovatiporus* Hill and Jones (ϵ)

Plate 32, figs. 1, 2

Favosites ovatiporus Hill and Jones 1940, pp. 199, 200, pl. 7, figs. 3, 4; pl. 8, figs. 1, 2; Hill *in* Thomas 1947, p. 41.

Favosites? *ovatiporus* Hill and Jones 1940 var.; Hill 1954, p. 113, pl. 8, figs. 21, 22.

Material. Specimens 15, 22, 28, 51, 52; figured slides T.S. 912 (28) and T.S. 961 (51).

Diagnosis. *F. squamuliferus* with large, ovate mural pores greater than 0.35 mm. in diameter, and well-spaced tabulae, usually less than 15 per cm.

Observations. As has been mentioned earlier the squamulae are so reduced in this forma that in places in a corallum they are virtually absent.

EXPLANATION OF PLATE 32

Longitudinal sections; all figures $\times 10$ and unretouched.

Figs. 1, 2. *F. squamuliferus* forma *ovatiporus* (ϵ). 1, T.S. 912 (28). Occasional large ovate mural pores, typically concave distant tabulae, and exceedingly small squamulae. 2, T.S. 961 (51). Stronger squamulae, closer tabulae, and smaller mural pores; i.e. intermediate between forma *bryani* and forma *ovatiporus*. Tyers River limestone.

Figs. 3–5. *F. squamuliferus* forma θ . 3, T.S. 944 (43) (also Pl. 33, fig. 11). Irregularly spaced mural pores, small squamulae, and expanding corallites which give rise to a subdigitate corallum which characterizes this forma. Note also comparatively thicker walls. 4, T.S. 930 (36). Intermediate between forma *nitidus* and forma θ . 5, T.S. 932 (37), (also Pl. 33, fig. 12). Larger corallite diameter again with small squamulae, thick walls, and irregularly distributed mural pores. Clear zones in the middle of the walls represent intermural spaces. Tyers River limestone.

Figs. 6, 7. *F. grandiporus* Etheridge. 6, T.S. 1208 (also Pl. 33, fig. 9, Pl. 34, fig. 4). Axial portion of a large cylindrical corallum. Note comparatively thin walls, well-spaced tabulae and mural pores, as well as small squamulae. 7, T.S. 1205. Distal portion of same corallum, showing strong thickening of the walls, heavier squamulae, and crowded tabulae. Mural pores are also smaller and more closely spaced. Lilydale Limestone.



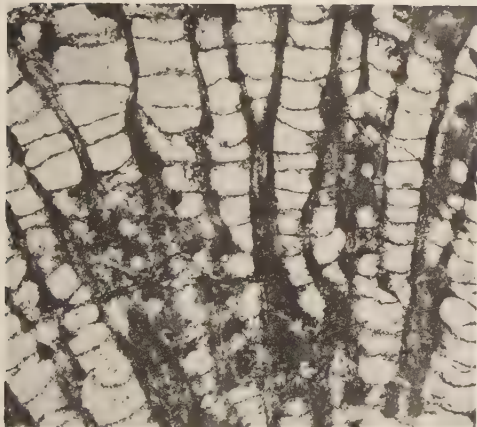
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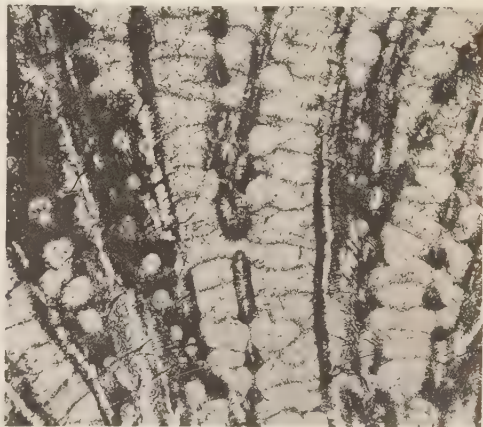
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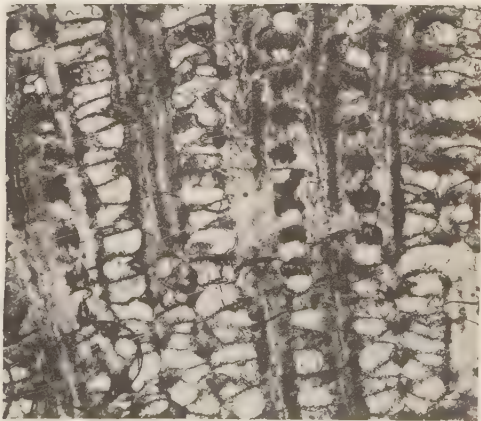
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F. squamuliferus forma ζ nov.

Plate 31, fig. 7

Diagnosis. *F. squamuliferus* with widely spaced tabulae and reduced squamulae as in *F. squamuliferus* forma *ovatiporus* but the mural pores are comparatively small and average 1.2 mm. apart.

Material. Specimen 30; figured slide T.S. 915 (30).

F. squamuliferus forma η nov.

Plate 30, fig. 8; Plate 33, fig. 4

Material. Specimen 14; figured slides T.S. 882-3 (14).

Diagnosis. *F. squamuliferus* with very thin walls averaging less than 0.01 mm. thick.

Observations. The single specimen from the Tyers limestone on which this forma is based shows consistently thin walls with a very narrow sporadic stereozone which may thicken slightly at the corners of the corallites. Other specimens (e.g. T.S. 967; Pl. 33, fig. 1) may show in places similar very thin walls, but this was the only specimen collected in which the feature was constant.

F. squamuliferus forma θ nov.

Plate 32, figs. 3-5; Plate 33, figs. 11, 12; Plate 34, fig. 5

Material. Specimens 36, 37, 43, 49; figured slides T.S. 943-4(43); T.S. 930(36); T.S. 931-2 (37); T.S. 1013.

Diagnosis. Subdigitate thick-walled *F. squamuliferus* with irregularly spaced mural pores and reduced squamulae.

Observations. This forma perhaps represents a morphological stage between *F. squamuliferus* and *F. grandiporus* since it possesses the subdigitate growth habit and thick walls of the latter species, although it lacks its characteristic distal thickening of the corallite walls.

Apart from the eight formae of *F. squamuliferus* recognized here, *F. salaebrosus* Ethridge should most probably be set aside as a ninth for forms of *F. squamuliferus* with reclined corallites.

It is considered that it is worth separating the species into the various formae since outside of a large collection one forma may appear to be separated from typical members of other formae by differences of specific merit.

COMPARISON OF *F. GRANDIPORUS* AND *F. SQUAMULIFERUS* WITH
NON-AUSTRALIAN SPECIES

Certain species have been described from the Upper Silurian to Middle Devonian limestones in Europe and Russia which fall in the morphological range of the species *F. grandiporus* and *F. squamuliferus* as these variable species must be understood. This list is probably by no means complete as the writer has been unable to trace most of the recent Russian literature and some of the more obscure European publications. It would

be of interest to establish whether these overseas species exhibit the same extreme variation as the Australian species. The species which have been found are:

(1) *Favosites brusnitzini* Peetz 1901, p. 177, pl. 3, fig. 11a, b. Chernyshev 1951, pp. 27–28, pl. 5, figs. 3–5, basal Devonian, Kuznetsk Basin. Chernyshev gives the corallite diameter of this species as between 0.5 and 1 mm., wall thickness 0.05 to 0.06 mm.; tabulae 9–16 in 5 mm., and the mural pores 0.2 mm. in diameter and about 0.5 mm. apart. The backed squamulae above the mural pores are apparent in Chernyshev's pl. 5, fig. 5. In all respects the neotype of this species chosen by Chernyshev cannot be distinguished from *F. squamuliferus* forma *bryani* Jones or forma *nitidus* Chapman.

(2) *Favosites intricatus* Barrande, Počta 1902 (Počta 1902, pp. 233–5, pl. 88, 91, 95, 102), Lower Devonian, Koněprus, Bohemia. The slides on pl. 102, figs. 2, 3 show a form indistinguishable from *F. squamuliferus* forma *bryani* or forma *nitidus* Chapman with well-developed squamulae. Squamulae do not appear to be present in the specimens illustrated on pl. 95; the septa are very much stronger and the mural pores are more often biserial than is usual in *F. squamuliferus*.

EXPLANATION OF PLATE 33

Transverse sections; all figures $\times 10$ and unretouched.

Figs. 1, 7, 8, 10. *F. squamuliferus* forma *nitidus* (β). 1, T.S. 967. Note variable wall thickness. Squamulae can be seen occurring back to back in adjacent corallites and occasional thin septal spines are also apparent. 7, T.S. 876 (9) (also Pl. 30, fig. 3). Poorly developed intermural spaces. 8, T.S. 925 (34) (also Pl. 30, fig. 4). Well-developed intermural spaces in the thickened angles of the corallites. 10, T.S. 870 (6). Constant diameter of walls and no rounding of corallites. Intermural spaces insignificantly developed. Tyers River limestone.

Fig. 2. *F. moonbiensis* Etheridge. T.S. 798 (also Pl. 31, fig. 3). Identical with *F. squamuliferus* forma *bryani* except in the absence of septal apparatus. Note the clear intermural spaces enlarging toward the corners of the corallites. Mudstone beneath the limestone, Tyers River.

Fig. 3. *F. squamuliferus* forma *bryani* (α). T.S. 891 (18). Blunt squamulae occurring back to back with discrete septal spines in some corallites. Tyers River limestone.

Fig. 4. *F. squamuliferus* forma η . T.S. 883 (14) (also Pl. 30, fig. 8). Form characterized by extremely thin walls. Tyers River limestone.

Fig. 5. *F. squamuliferus* forma *australis* (δ). T.S. 934 (39) (also Pl. 30, fig. 6). Form characterized by subcrioid growth. Note wide separation of corallites in places and 'stellate' intermural spaces present in parts of the figure. Tyers River limestone.

Fig. 6. *F. squamuliferus* forma *stelliformis* (γ). T.S. 1210 (also Pl. 30, fig. 2). Well-developed 'stellate' intermural spaces at corners of corallites and thickening of corallite walls in their vicinity. Lilydale Limestone.

Fig. 9. *F. grandiporus* Etheridge. T.S. 1209 (also Pl. 32, figs. 6, 7; Pl. 34, fig. 4). Section cut toward distal region of corallum. Note 'stellate' intermural space in top left of figure showing thickening and bleaching of the stereome of the corallites in its immediate vicinity. Lilydale Limestone.

Figs. 11, 12. *F. squamuliferus* forma θ . 11, T.S. 943 (43) (also Pl. 32, fig. 3). Rounding of corallites and bleaching of stereome in vicinity of intermural spaces. 12, T.S. 931 (37) (also Pl. 32, fig. 5). Thick-walled form showing well-developed intermural spaces and rounding of corallites. Tyers River limestone.

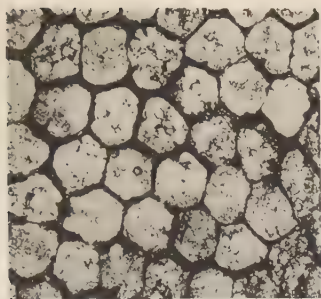
EXPLANATION OF PLATE 34

Figs. 1, 2. *F. squamuliferus* forma *nitidus* (β). 1, T.S. 1031. Corallum showing a growth zone approaching forma *ovatiporus* with increase of spacing of tabulae, reduction of the squamulae and development of large, distant, ovate mural pores. $\times 5$. 2, T.S. 967. Corallum showing variation of corallite diameter and wall thickness. Tyers River limestone. $\times 5$.

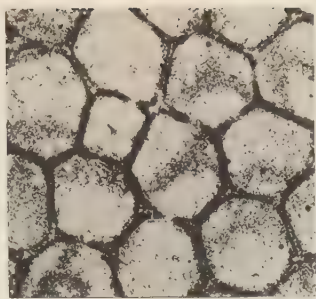
Fig. 3. *F. squamuliferus* forma *australis* (δ). T.S. 985. Widely developed intermural spaces occurring at similar heights between adjacent corallites. Tyers River limestone. $\times 5$.

Fig. 4. *F. grandiporus* Etheridge. T.S. 1209. Well-developed 'stellate' intermural spaces. Lilydale Limestone. $\times 20$.

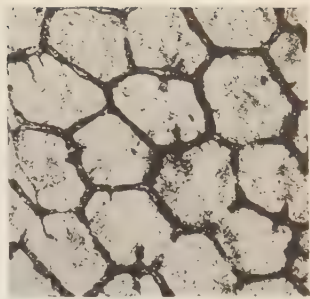
Fig. 5. *F. squamuliferus* forma θ . T.S. 1013. Irregularly developed intermural spaces with bleaching of the stereome of the corallites in their vicinity. Tyers River limestone. $\times 20$.



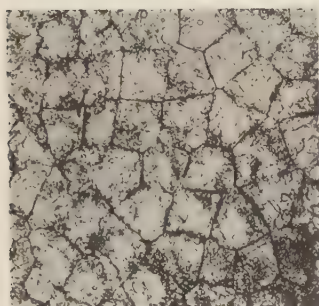
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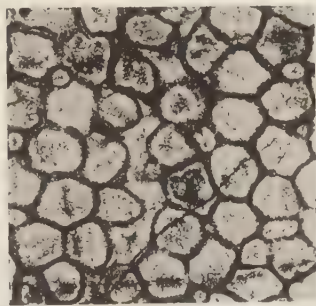
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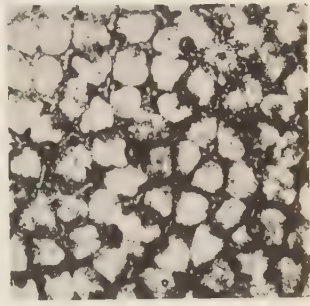
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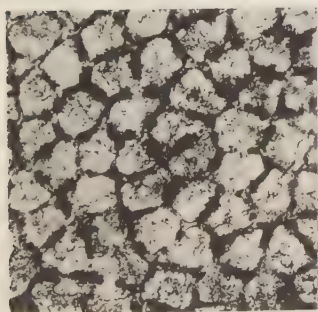
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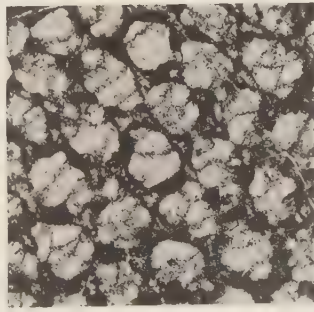
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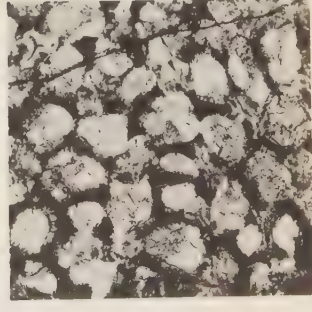
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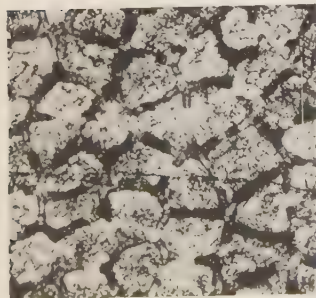
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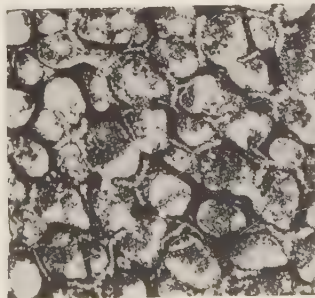
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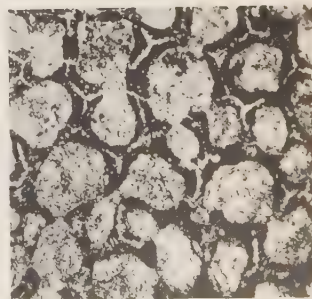
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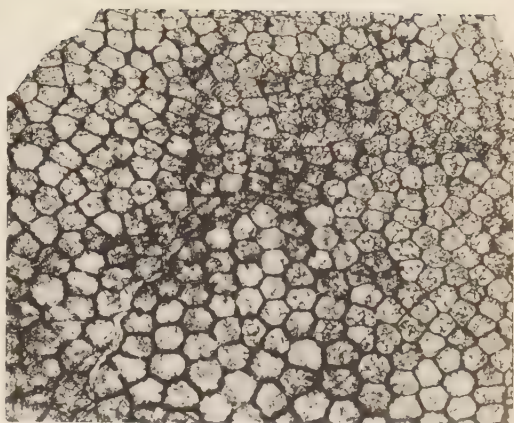
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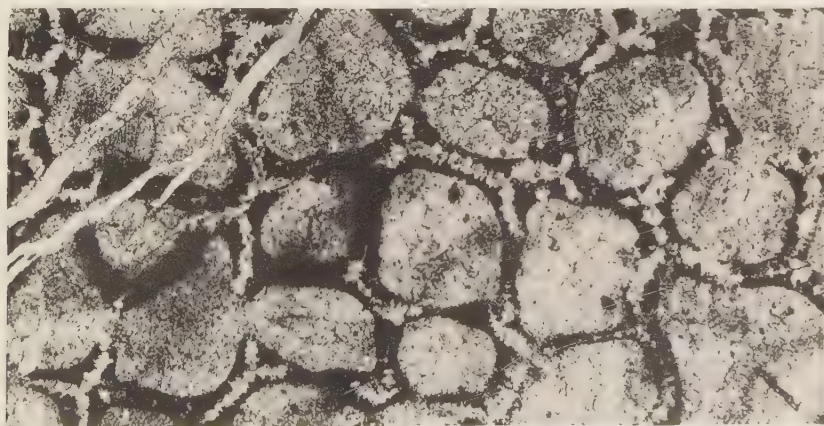
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- (3) *Favosites proasteriscus* Charlesworth 1914, pp. 373–4, pl. 33, fig. 1a, b; Lower Devonian, Carnic Alps. This species, with corallites 1 mm. in diameter, possesses intermural deposits similar to those of the Australian species. Charlesworth speaks of the ‘undulating’ character of the corallites in longitudinal sections, stating that in this respect the species is similar to *F. intricatus* Barrande. This suggests that the species may be squamulate, in which case the species shows strong affinities to *F. squamuliferus* forma *bryani*. If it is not, the species bears a close relationship to *F. moonbiensis* although the tabulae are much closer in *F. proasteriscus*. Charlesworth states there are twenty-five tabulae per cm., but his plate shows about fifty. *F. interstinctus* Regnéll 1941 from the Siluro-Devonian of Chöl-tagh, eastern Tien-shan, is also a species close to *F. moonbiensis*.
- (4) *Alveolites (Caliapora) frechi* Charlesworth 1914, p. 381, pl. 34, fig. 1a, b. Lower Devonian, Carnic Alps. This species, with a corallite diameter of about 0.5 mm., appears very similar to forms included here in *F. squamuliferus* forma *nitidus* although it is impossible to arrive at any real understanding of the species from Charlesworth’s description and figures.
- (5) *Alveolites (Caliapora) carnicus* Charlesworth 1914, p. 396, pl. 34, fig. 2. Upper Silurian, Carnic Alps. Again it is very difficult to interpret this species with a corallite diameter of about 1 mm. and strong squamulae. The form figured, however, appears to be closely related to *F. squamuliferus* forma *bryani* or the thick walled subdigitate forma *θ*.
- (6) *Favosites inosculans* Nicholson; Le Maitre 1931, pp. 575–7, pl. 29, figs. 1–4. non *Favosites? inosculans* Nicholson 1881, pp. 20–21, pl. 1, figs. 4, 4a. Upper Lower Devonian; Bassin d’Ancenis. The form illustrated by Le Maitre is closely comparable with *F. squamuliferus* forma *nitidus* in all respects except perhaps that the form of growth is more reminiscent of *F. squamuliferus* forma *θ*.
- (7) *Favosites alpina* (Hornes) Penecke; Le Maitre 1934, p. 171, pl. 8, figs. 7–9. non *Favosites alpinus* Penecke 1894, vide Schouppé 1954b, pp. 25–26, pl. 1, figs. 4, 10. Upper Lower Devonian; Bassin d’Ancenis. Although Le Maitre did not describe the mural pores in this form, they appear to be uni-serial in her plate. In every other respect this form falls within the range of *Favosites squamuliferus* forma *bryani*.
- (8) *Favosites inosculans* Nicholson; Le Maitre 1937, pp. 113–14, pl. 8, figs. 1–3. non *Favosites? inosculans* Nicholson 1881. Lower Middle Devonian, Ville-de-d’Ardin. Le Maitre’s figures are of a form indistinguishable from *F. grandiporus* Chapman showing distally pronounced thickening of the corallite walls, strongly developed squamulae as well as crowded tabulae. The dimensions of the form illustrated fall within the range of *F. grandiporus*.
- (9) *Favosites festivus* Chernyshev 1951, p. 26, pl. 5, figs. 1, 2. Upper Silurian, Kuznetsk Basin. Chernyshev gives the corallite diameter of this species as between 0.4 to 0.5 mm.; tabulae 20 to 25 per mm.; mural pores ovate 0.15 to 0.24 mm. in diameter and less than 0.5 mm. apart. Small squamulae above the mural pores are seen in Chernyshev’s figure. This species is very closely comparable to *F. squamuliferus* forma *stelliformis*. In transverse sections the walls of the corallites have a much stronger inosculating appearance in Chernyshev’s species, apparently due to pores being developed at the same height in adjacent corallites. Chernyshev compares this species with *Favosites fistulosis* (Chernyshev 1937, p. 76, pl. 4, fig. 1a, b, a reference unavailable to me in Australia). He notes that *F. festivus* differs from *F. fistulosis* in bigger corallites (0.6 to 0.8), fewer tabulae, and smaller, not so variable mural pores. If these are the only differences, then *F. fistulosis* is identical with *F. squamuliferus* forma *nitidus*.
- (10) *Favosites endygashensis* Chernyshev 1951, p. 36, pl. 12, figs. 1, 2. Middle Devonian, Kuznetsk Basin. Chernyshev gives the dimensions of this species as corallites 1 to 1.6 mm. in diameter with thick walls 0.1 to 0.2 mm. apart; 7 to 12 tabulae in 5 mm., the mural pores 0.3 mm. in diameter about 0.5 mm. apart. Further, the corallum is said to be ‘tree-like, with short branches’. Thus this thick-walled abramose form is comparable with *F. squamuliferus* forma *θ*. Closely comparable squamulae are also to be seen in Chernyshev’s figure. *Pachypora crassiramosa* Chernyshev 1951 is a very closely related form with larger corallites between 1.5 and 2 mm. in diameter.
- (11) *Alveolites (Caliapora) heritschi* Schouppé 1954a, pp. 422–4, pl. 27, fig. 22. Lower Devonian, Carnic Alps. This species, with its corallite diameter about 0.6 mm. appears to be closely comparable with *F. squamuliferus* forma *nitidus*. However, in the character of the mural pores it may differ from *F. squamuliferus* for Schouppé remarks that the pores, although large, are not frequent.

It is noteworthy that the time range of the forms overseas which fall within the morphological range of *F. squamuliferus* is virtually identical with the time range of the

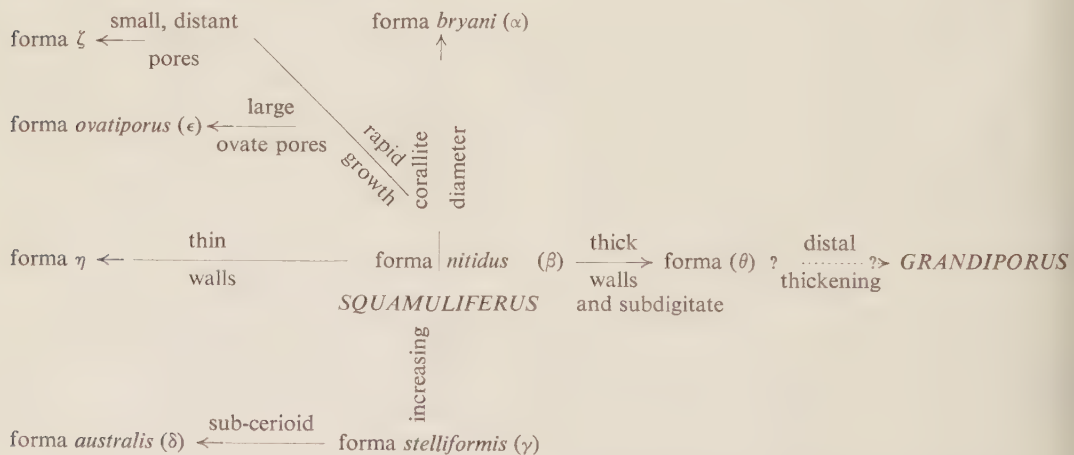
species in Australia—from Middle or Upper Silurian to Middle Devonian. The undoubted Silurian occurrences in Victoria are from the Eildon district where Hill recorded the presence of '*F. ovatiporus*' from a limestone lens which occurs beneath the horizon of *Monograptus uncinatus*, and from the Middle (?) Silurian of the Cowombat Creek from which Chapman (1920) illustrated a form as '*Favosites gothlandica*' (pl. 23, figs. 18, 19) which is identical with *Favosites squamuliferus* forma *bryani*. Again with *F. grandiporus*, which in Australia is only known from the Lilydale Limestone, of probable upper Lower Devonian age, Le Maitre (1937) illustrated an identical form from the basal Middle Devonian of France.

REMARKS ON THE VARIATION IN *F. SQUAMULIFERUS*

Discussion of the causes of variation in fossil species must at the best be conjectural. Thus detailed analyses within the framework applicable to modern forms (e.g. Mayr, Linsley, and Usinger 1953) have little value, although such frameworks are interesting inasmuch as they cover all the possible causes of intra-specific variation.

A major point which has arisen from the occurrences of species in the fauna analysed in detail is that it appears that squamulae were developed in this group as a response to major environmental changes; the species *F. moonbiensis* is confined to what was presumably a muddy environment, whereas *F. squamuliferus* and its formae are characteristic of a limestone environment.

Two of the formae appear to have arisen due to differential growth. These are *F. squamuliferus* forma *ovatiporus* (ϵ) and forma ζ , and presumably include coralla which grew more rapidly than those of the more typical formae. Again the development of wide intermural spaces in *F. squamuliferus* forma *australis* (δ) was probably caused by adverse environmental conditions.



MORPHOLOGICAL RELATIONSHIP OF THE SPECIES AND FORMAE OF AUSTRALIAN SQUAMULATE FAVOSITIDS

However, the extreme variability, for example in corallite diameter, must have stemmed from genetic variability of the species; a certain degree of this variation perhaps could be ascribed to micro-environmental differences, but it is impossible to trace

these in a limestone which is basically an accumulation of reworked organic débris. In this respect it should be noted that other species of *Favosites* occurring side by side with *F. squamuliferus* show very little variation.

The possibility cannot be overlooked that there is present in the fauna more than one species of squamulate favositid, the ranges of variation of which overlap, but only an arbitrary subdivision into formae could be achieved. Detailed work on the younger horizons in which *F. squamuliferus* occurs may establish that in those horizons stable groups are present in the species within its presently defined range of variation. Until this is done it is best to divide the species merely into formae.

Acknowledgement. I am indebted to Dr. Dorothy Hill of the University of Queensland who read and criticized the manuscript.

Addendum. Since this manuscript was submitted for publication the writer has had the opportunity to study B. S. Sokolov's (1955) monograph on tabulate corals. Lengthy comment cannot be made here; suffice to say that to co-ordinate this present work with Sokolov's taxonomic level the genus used here should be regarded as a sub-order or family, and the species as families or genera. However, this is not possible in terms of Sokolov's classification as the three species mentioned here, and regarded by the present writer as very closely related, overlap three of Sokolov's 'sub-orders', namely the Favositina (*F. moonbiensis* Eth.), the Thamnoporina (*F. grandiporus* Eth.), and the Alveolitina (*F. squamuliferus* Eth.).

Sokolov, furthermore, holds that the stellate intermural spaces as seen in *Asteriophyllum ænigmaticum* Orfiev and *Favosites stellaris* Chernyshev were caused by symbiotic worms. Although this can be argued for such forms of *Favosites* as those where definite tubules are present within the corallite walls as in the 'genera' *Gephuropora*, *Parafavosites*, &c.), this interpretation does not appear to be applicable to the wall structures of the species group described here.

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NEW SPECIES OF BRACHIOPODS FROM THE UPPER DEVONIAN OF HAY RIVER, WESTERN CANADA

by A. E. H. PEDDER

ABSTRACT. *Nervostrophia borealis*, *N. maclareni*, and *Cyrtina lapidea* are described and figured as new species from the Hay River formation of the North West Territories, Canada. *Douvillinella? crickmayi* is described and figured as a new species from the lower Grumbler formation of the same area. All the fossils are of Frasnian age.

THE fossils described were collected by Dr. P. E. Kent of BP Exploration (Canada) Limited and by Dr. E. W. Best, R. L. Pemberton, and A. E. H. Pedder of Triad Oil Co. Ltd. in June 1958. The author is much indebted to these companies for permission to publish the work and to present the type specimens to the Geological Survey of Canada.

Biostratigraphy. Stratigraphical thicknesses in the Hay River area have mostly been obtained from scattered incomplete river sections and various published estimates differ considerably. Warren and Stelck (1950, p. 68) gave the thickness of the type Hay River formation (as later restricted by Crickmay) as about 270 feet; Crickmay's figure for the same interval is 630 feet (1957, p. 6). Farmilo is quoted by Law (1955, p. 1977) as having measured about 900 feet of Hay River shale on Hay River and deWit (unpublished) has obtained for Triad Oil Co. Ltd. a total thickness of 1,250 feet for the Hay River shales. Both of these latter measurements include Crickmay's Simpson formation, but, even so, indicate a thickness in excess of 630 feet for the type Hay River formation (restricted). Bore-hole evidence (Law 1955, fig. 5) also indicates a greater thickness than quoted by Crickmay.

The new species were obtained from three beds. The lowest is a grey argillaceous limestone grading to a pure coquina bed in part, and is exposed on Hay River opposite mile 14 of the Mackenzie Highway (Grimshaw Road). Part of its fauna is: *Eliasopora* sp., *Hederella* sp., *Orbiculoidea* sp., *Productella* sp., *Nervostrophia borealis* sp. nov., *Monelasma besti* Pedder, *Schizophoria* sp., *Atrypa* sp., *Spinatrypa* sp., *Eleutherokomma reidfordi* Crickmay, *Cyrtospirifer* [= *Regelia*] *glaucus* Crickmay, *Cyrtina lapidea* sp. nov., *Spirorbis* sp., *Tentaculites mackenziensis* Kindle, ostracods, and a trilobite. The horizon is the lowest assigned to the Hay River formation as restricted by Crickmay.

The second bed is a limestone exposed just above Louise Falls on Hay River. Stratigraphically it is immediately below the topmost shale and siltstone of the Hay River formation and is currently regarded as being from 30 to 40 feet below the top of that formation. The rock is very fossiliferous, but only those specimens exposed are easily collected and these are generally water worn. Part of the fauna is: *Macgeea proteus* Smith, *Nervostrophia maclareni* sp. nov., *Productella* sp., *Atrypa* sp., *Cyrtospirifer* sp., *Adolfia* sp., pelecypods, *Tentaculites* sp., *Devonocidaris* sp., and *Decadocrinus* sp.

The highest bed is a maroon argillaceous limestone exposed on Hay River opposite mile 38 of the Mackenzie Highway. It is near the base of the Grumbler formation and

The following is part of the bed's fauna: *Clionoides* sp., *Spongophyllum imperfectum* Smith, *Aulocaulis* sp., *Thamnopora* sp., *Vinelloidea* sp., *Leptotrypella* sp., *Hederella* sp., *Ternodia* sp., *Petrocrania* sp., *Stropheodonta* sp., *Douvillinella?* *crickmayi* sp. nov., *Schuchertella* sp., *Schizophoria* sp., *Gypidula* sp., *Atrypa rubromitra* Crickmay, *A. spp.*, *Cyrtospirifer* sp., *Tenticospirifer* sp., *Adolfia* spp., *Cyrtina* sp., *Cranaea* sp., pelecypods, cephalopods, *Cornulites* sp., *Spirorbis angulosus* Fenton and Fenton, crinoid fragments.

SYSTEMATIC PALAEONTOLOGY

Superfamily STROPHOMENACEA Schuchert 1896

Family STROPHEODONTIDAE Caster 1939

Genus NERVOSTROPHIA Caster 1939 emended Williams 1953

Neoholotype (by author's original designation) *Stropheodonta nervosa* Hall = *Strophomena nervosa* Hall 1843, text-figs. 1, 1a on p. 266, Chemung group, Bath and Campbelltown, New York.

Nervostrophia borealis sp. nov.

Plate 35, figs. 1-10

1950 *Douvillinaria variabilis* (Calvin); Warren and Stelck, p. 69.1956 *Douvillinaria variabilis* (Calvin); Warren and Stelck, pl. 16, fig. 26.1959 *Nervostrophia* sp. Pedder, p. 472.Non *Douvillinaria variabilis* Calvin sp.*Type derivation.* Latin, *borealis* = northern.

Types. Holotype, specimen originally Triad Oil Co. Ltd. collection no. X46e, now Geological Survey of Canada type no. 14,598. Six paratypes, specimens originally Triad Oil Co. Ltd. collection nos. 14,599-14,604, now Geological Survey of Canada type nos. 14,599 to 14,604.

Type stratum. Hay River formation, coquina bed 630 feet below top (Crickmay 1957, p. 6; not 1953, p. 11); Upper Devonian, Frasnian.

Type locality. Canada, North West Territories, Hay River opposite mile 14 of the Mackenzie Highway measured south-westward, about 80 feet above water-level and 10 feet below bank top. Latitude 60° 41' N., longitude 115° 54' W.

Description. Shell small and fragile. Profile plano-convex. Outline semicircular anteriorly, posteriorly just flexed at pedicle beak, cardinal extremities with small mucrones, postero-lateral margins weakly concave. Anterior commissure rectimarginate. Shell substance very thin, calcitic and pseudopunctate.

Pedicle valve weakly convex centrally and postero-centrally, plane near lateral and anterior margins. Umbonal region, small, longer than broad and only slightly elevated. Beak minute and blunt. Beak ridges sharp along entire length. Interarea plane, apsaal, very broadly equilaterally triangular with an apical angle of about 168°. Deltidialium open anteriorly, closed posteriorly by a strongly medianly arched pseudodeltidialium. Hinge-line straight, denticulate along most of its length in young valves and for about two-thirds of its length in adults. Process pits deep as thin shell permits, slightly posteriorly directed. Ventral process low and narrow. Muscle scars petal-shaped, about one-half as long as the valve, lightly impressed, bounded postero-laterally by heavy ridges, open antero-laterally and anteriorly. Adductor and diductor scars not differentiated in the type specimens. Median septum very fine, about one-half the length of the muscle scars. Interior surface, with the exception of the muscle scars and cardinalia, entirely and finely papillose; postero-lateral muscle bounding ridges less finely papillose.

External surface ornament variable, of more or less continuous, generally straight, rarely sinuous costae, separated by from one to four intercalated costellae; costellae rare in gerontic specimens; costae and costellae number about seven per millimetre near margins of valve. Concentric micro-fila superimposed on entire surface, numbering about fifteen per millimetre. Interarea with growth striae parallel to hinge-line and with clear traces of denticles, especially anteriorly.

Brachial valve plane. Umbo and beak not developed. Interarea linear. Notothyrium displaced by cardinalia. Chilidium degenerate. Hinge-line straight, socketed opposite denticles of pedicle valve. Cardinal process lobes, stout, disjunct, with attachment faces posteriorly directed. Socket plates small, attached to and parallel to cardinal process lobes. Muscle scars subtriangular, lightly impressed, bounded postero-laterally by large hummocks divergent 90° to each other, open anteriorly; each muscle divided anteriorly by low, broad, elongate elevations parallel to postero-lateral muscle ridges. Median septum broad posteriorly, rapidly tapered to a fine ridge anteriorly, three-fourths the length of the valve. Interior surface, with the exception of the cardinalia and deeper parts of muscle scars, finely and irregularly papillose; postero-lateral muscle ridges and elevations in anterior part of muscles less finely papillose; exterior ornament similar to that of pedicle valve, but costae less developed and approaching the size of the costellae. Denticle sockets visible from exterior through a thin shell layer.

Dimensions (partly reconstructed and estimated from the contour of the concentric micro fila). Holotype, paratypes 2, 4 (pedicle valves), and 5 (brachial valve), length 11.4, 5.1, 5.4, and 5.0 mm., width 14.0, 8.0, 8.3, and 6.6 mm., depth 1.3, 1.1?, and 0.1 (not including depth of process lobes) mm.

Remarks. No similar fossil has been named from the Upper Devonian. The species superficially resembles *Douvillina variabilis* (Calvin) from the Independence formation of Iowa, but is not congeneric with it.

Nervostrophia maclareni sp. nov.

Plate 36, figs. 1-5

Name derivation. Patronym for Dr. D. J. McLaren, Geological Survey of Canada, Ottawa.

Types. Holotype, specimen originally Triad Oil Co. Ltd. collection no. X38s, now Geological Survey of Canada type no. 14,605. Three paratypes, specimens originally Triad Oil Co. Ltd. collection nos. X38t-v, now Geological Survey of Canada type nos. 14,606 to 14,608.

Type stratum. Hay River formation, upper unnamed siltstone, shale, and limestone unit, 30 to 40 feet below the top of the formation (Crickmay, 1957, p. 6; not 1953, p. 11); Upper Devonian, Frasnian.

Type locality. Canada, North West Territories, a few feet above Louise Falls on Hay River. Latitude $60^\circ 30' N.$, longitude $116^\circ 14' W.$

Description. Shell large and thin for genus. Profile plano-convex. Outline variably sub-semicircular. Hinge-line straight, cardinal extremities strongly mucronate, postero-lateral margins moderately concave. Anterior margin rectimarginate. Shell substance very thin, calcitic and pseudopunctate.

Pedicle valve very weakly convex, mostly plane, but anterior and lateral margins slightly convex. Umbonal region very slightly inflated. Beak minute and blunt. Beak ridges sharp along entire length. Interarea very broadly equilaterally triangular, plane surfaced. Nature of delthyrium and its cover not revealed in the primary material.

hinge line denticulate for about 75 per cent. of its length. Process pits shallow. Nature of cardinalia and musculature not revealed in the primary material. Internal ornament centrally finely and closely papillose with traces of the external ornament visible near the margins. External ornament of continuous, straight, or slightly sinuous costae developed from costellae, latter number from two to nine, generally five, between each costae; costae and costellae number about six per millimetre near the margins of the valve. Faint concentric micro-fila superimposed on most, if not all, the surface.

Brachial valve plane. Umbo not developed. Beak represented by a minute projection at the base of the cardinal process. Notothyrium displaced by cardinalia. Chilidium probably degenerate. Hinge-line socketed opposite the denticles of the pedicle valve. Cardinal process lobes not well preserved in type material, disjunct, with attachment faces posteriorly directed. Socket plates larger than average relative size for the genus, attached to and divergent from, the cardinal process lobes. Muscle scars small, petal-shaped, superficial, bounded postero-laterally by large crescent-shaped hummocks, open in other directions. Median septum degenerate. Postero-lateral muscle bounding hummocks strongly papillose, other parts of the interior surface not markedly papillose, external ornament visible from the interior near the valve margins. External ornament similar to that of the pedicle valve. Denticle sockets visible from the exterior through a very thin shell layer.

Dimensions. Holotype and paratype 3, length 20.0 and 13.5 mm., width (less mucrones) 5.8 and 25.0 mm. (with mucrones)? and 36.0 mm. depth (pedicle valve only) 1.5 and 2 mm.

Remarks. In several respects this species is not typical of *Nervostrophia*. The shell is exceptionally thin and delicate, a median septum is scarcely developed in the brachial valve; the relatively large, divergent socket plates and unimpressed muscle scars of the brachial valve are also exceptional for the genus.

From *Nervostrophia calvini* Stainbrook, occurring in the Independence formation of Iowa, this species is distinguished by its lack of a strong geniculation near the anterior and antero-lateral commissure and also, perhaps, by internal details, which have not been illustrated for *N. calvini*.

From *N. vestita* Crickmay, occurring lower in the Hay River formation on Hay River, this species is distinguished by its shorter median septum and postero-lateral muscle bounding ridges in the pedicle valve and by its less nervose surface ornament.

Genus DOUVILLINELLA Priestersbach 1926 emended Williams 1953

Enoholotype (by monotypy) *Douvillina filifer* Schmidt 1913, pp. 313, 314, pl. 23, figs. 1a-7. *Cultrigatus* zone (Couvinian, or lower Middle Devonian), südlich der Attendorn-Elsper Doppelmulde, Germany.

Remarks. Priestersbach proposed *Douvillinella* as a subgenus of *Stropheodonta*, differing from that genus by possession of brace plates (Stützplatten) and in having concave ventral and convex dorsal valves instead of convex ventral and concave dorsal valves. The species described below is associated with *Douvillinella* only because it is a resupinate *douvillina*-like stropheodontid. It is possibly not congeneric with *Douvillina filifer* Schmidt.

Douvillinella? crickmayi sp. nov.Plate 36, figs. 7-11; text-fig. 1*n*1950 *Strophonella* sp. Warren and Stelck, p. 67.*Name derivation.* Patronym for Dr. C. H. Crickmay, Imperial Oil Ltd., Calgary, Alberta.*Types.* Holotype, specimen originally Triad Oil Co. Ltd. collection no. X28v, now Geological Survey of Canada type no. 14,609. Four paratypes, specimens originally Triad Oil Co. Ltd. collection nos. X28w-z, now Geological Survey of Canada type nos. 14,610 to 14,613.*Type stratum.* Grumbler formation, maroon argillaceous limestone about 80 feet above the base of the formation; uppermost Frasnian.*Type locality.* Canada, North West Territories, Hay River opposite mile 38 of the Mackenzie Highway (Grimshaw Road), measured south-westward. Latitude 60° 29' N., longitude 116° 19' W.*Description.* Shell small and robust. Profile very gently resupinate, concavo-convex immediately anterior of hinge, convexi-plane or just convexi-concave centrally, biconvex near anterior margin (text-fig. 1*n*). Outline semicircular anteriorly, postero-lateral margins nearly straight, cardinal extremities with small mucrones. Anterior commissure rectimarginate. Shell substance relatively thick, calcitic and pseudopunctate.

Pedicle valve almost plane, very gently convex umbonally, plane or just concave centrally, very gently convex near anterior and lateral margins. Umbonal region feebly developed. Beak minute, projecting only very slightly. Beak ridges sharp along entire length. Inter-area plane, apsaclinal, subrectangular. Delthyrium equilaterally triangular with an

EXPLANATION OF PLATE 35

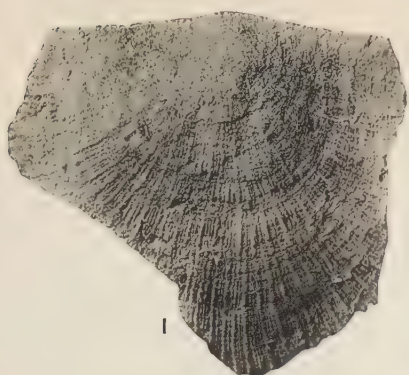
All illustrations unretouched, photographed by K. S. Wilson. Specimen numbers refer to Geological Survey of Canada type numbers. All specimens are from the Hay River coquina bed, Hay River opposite mile 14 of the Mackenzie Highway, North West Territories, Canada.

Figs. 1-10. *Nervostrophia borealis* sp. nov. 1, 2, Holotype, 14,598, external and internal pedicle views, $\times 4$ and $\times 4$. 3, 4, Paratype 2, 14,600, internal and external views, $\times 5$ and $\times 5.6$. 5, 6, Paratype 3, 14,603, external and internal brachial views, $\times 4.3$ & $\times 4$. 7, Paratype 3, 14,601, lateral brachial view, $\times 4$. 8, Paratype 4, 14,602, external pedicle view, $\times 4$. 9, Paratype 1, 14,599, internal brachial view, $\times 4$. 10, Paratype 6, 14,604, external brachial view, $\times 4$.Figs. 11-17. *Cyrtina lapidea* sp. nov. 11-13, Holotype, 14,614, anterior view, $\times 4$, anterior view, $\times 2$, brachial view, $\times 1$. 14, 15, Paratype 1, 14,615, lateral view, $\times 3.5$, posterior view, $\times 3.6$. 16, 17, Paratype 2, 14,616, internal view, $\times 4$, external view, $\times 2$.

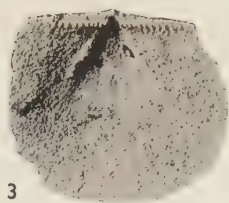
EXPLANATION OF PLATE 36

All illustrations unretouched, photographed by K. S. Wilson. Specimen numbers refer to Geological Survey of Canada type numbers.

Figs. 1-5. *Nervostrophia maclareni* sp. nov., 30-40 feet below top of the Hay River formation, a few feet above Louise Falls on Hay River, North West Territories, Canada. 1, 2, Holotype, 14,605, external pedicle views, $\times 1$ and $\times 2$. 3, Paratype 1, 14,606, internal brachial view, $\times 2$. 4, Paratype 2, 14,607, external brachial view (left side of crack) and external pedicle cast (right side of crack), $\times 2$. 5, Paratype 3, 14,608, external pedicle view (partly obscured by matrix), $\times 1.8$.Fig. 6. *Cyrtina lapidea* sp. nov., Hay River formation coquina bed, Hay River opposite mile 14 of the Mackenzie Highway, North West Territories, Canada, paratype 3, 14,617, external brachial view, $\times 2.4$.Figs. 7-11. *Douvillinella? crickmayi* sp. nov., about 80 feet above the base of the Grumbler formation, Hay River opposite mile 38 of the Mackenzie Highway, North West Territories, Canada. 7, 8, Holotype, 14,609, external and internal pedicle views, $\times 2$ and $\times 2$. 9, Paratype 4, 14,613, external brachial view, $\times 2$. 10, Paratype 3, 14,612, external pedicle view, $\times 5$. 11, Paratype 1 (right), 14,610, internal brachial view and paratype 2 (left), 14,611, internal pedicle view, $\times 2$.



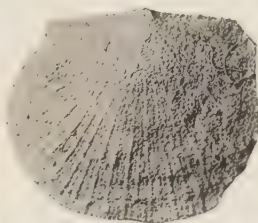
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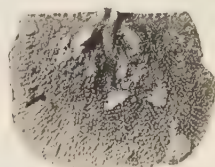
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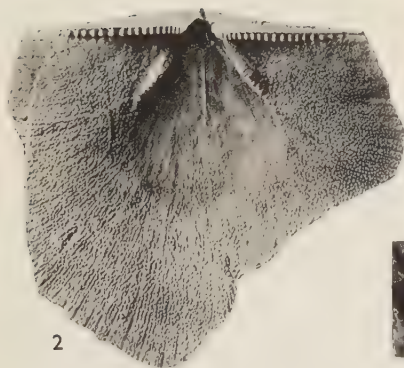
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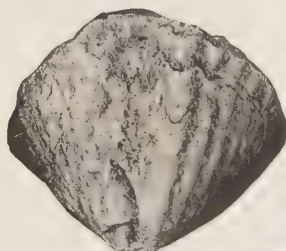
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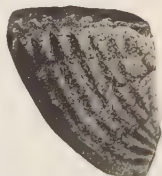
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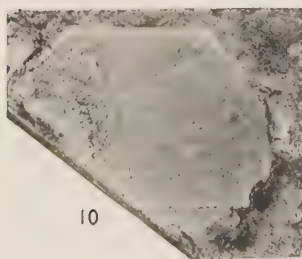
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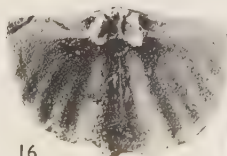
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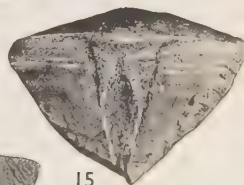
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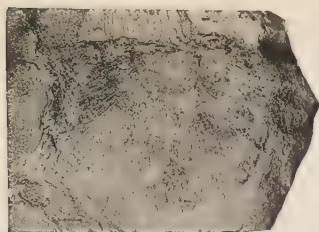
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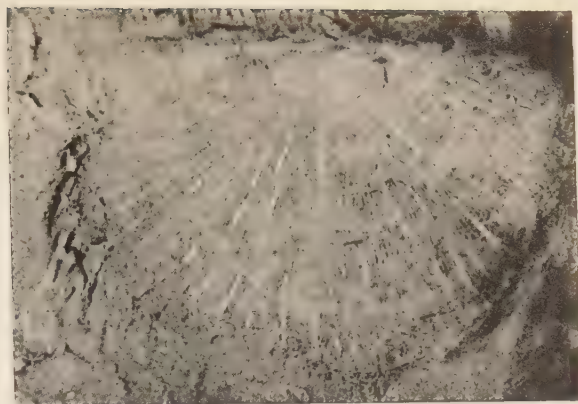
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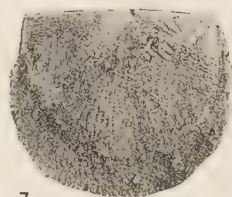
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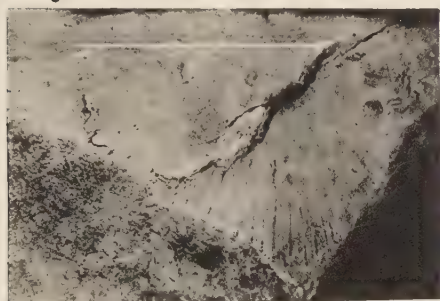
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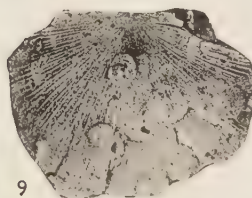
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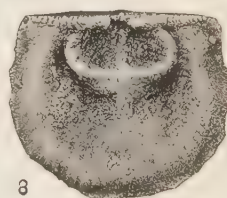
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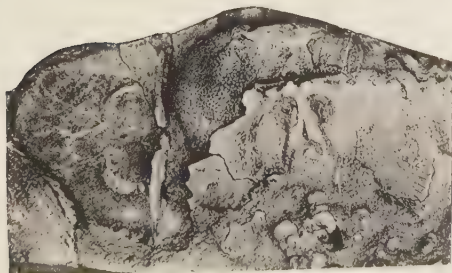
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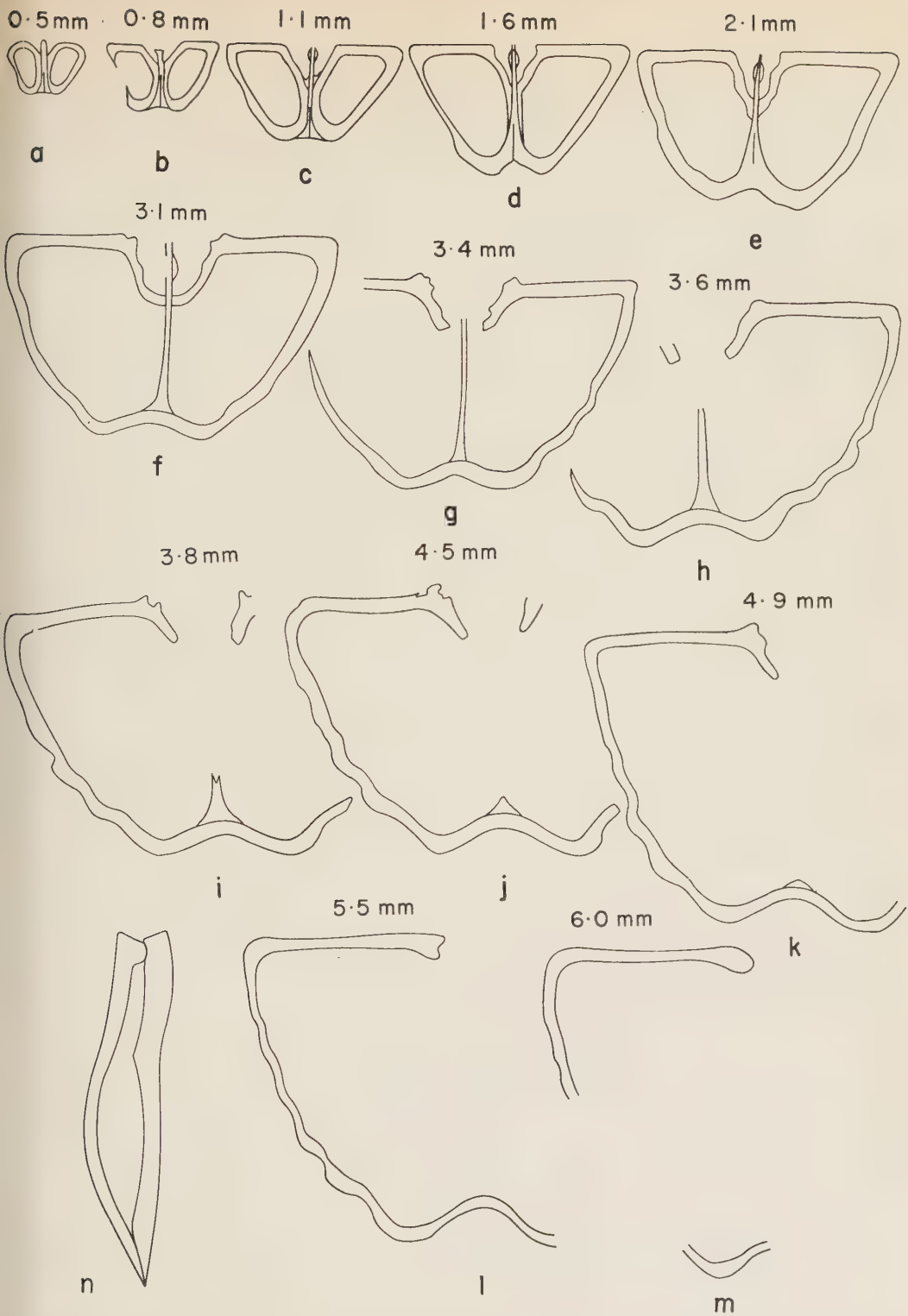
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TEXT-FIG. 1. a-m, *Cyrtina lapidea* sp. nov., Hay River formation coquina bed, Hay River opposite mile 14 of the Mackenzie Highway, North West Territories, Canada, paratype 4 (now destroyed), series of sections of pedicle valve, $\times 10$, measurements above each figure indicate distance from beak. l, *Douvillinella? crickmayi* sp. nov., diagrammatic but based on holotype and paratypes, longitudinal section, $\times 5$.

apical angle of about 12° , entirely closed by a completely and strongly arched pseudodeltidium. Hinge-line straight, denticulate along entire length. Process pits deep, slightly posteriorly directed. Ventral process robust, anteriorly prolonged to a fine low median ridge, extending to the anterior edge of the muscle scars. Muscle scars prominent, elevated to the form of a saucer, posterior edge at a variable angle of about 20° with the hinge-line, anterior edge parallel with hinge-line, lateral margins rounded, more sharply so laterally than anteriorly. Interior surface, apart from the muscle scars and cardinalia, finely and evenly papillose; cardinalia smooth, muscle scars with faint radial striations. External ornament of fine, variable, primary and intercalated costae of different sizes, numbering about six per millimetre at the poster-lateral margins and about four per millimetre at the anterior margin of adult valves. Growth lines strong, but developed only near the margins of some valves. Interarea smooth with faint traces of denticles visible anteriorly.

Brachial valve generally very slightly concave immediately anterior of the central part of the hinge-line, gently convex elsewhere (text-fig. 1*n*). Outline similar to that of the pedicle valve, but less or not mucronate. Umbo and beak not developed. Interarea apsaclinal and almost linear. Notothyrium displaced by cardinalia. Chilidium vestigial, gently convex. Hinge-line straight, socketed opposite the denticles of the pedicle valve. Cardinal process lobes of average size, disjunct, with attachment faces posteriorly directed. Muscle scars asymmetrically petal-shaped with long narrow extensions parallel to and laterally adjacent posteriorly, to the brace plates, deeply impressed. Median septum broad, relatively low, anteriorly bifurcated, bifurcated parts confluent with the elongated brace plates. Interior surface of cardinalia smooth, muscle scars without papillae, but irregularly pitted, rest of central part of surface finely and evenly papillose. Valve borders with clear traces of surface costae. Exterior surface ornament same as that of pedicle valve with denticle sockets visible through a very thin shell layer.

Dimensions. Holotype (dissociated pedicle valve) and paratype 4 (dissociated brachial valve), length 12.1 and 11.8 mm., width 14.1 and 15.5 mm., depth 1.9 and 1.8 mm.

Remarks. *Strophonella* does not occur in the Grumbler formation. Warren and Stelck (1950, p. 67) were probably referring to this species, since it is common in the lower Grumbler maroon beds, while other resupinate strophodontids are either rare or absent. No similar species has been named.

Superfamily PUNCTOSPIRACEA Cooper 1944

Family CYRTINIDAE Stehli 1954

Genus CYRTINA Davidson 1858

Genoelectotype (by Dall 1877, p. 24). *Cyrtia heteroclita* DeFrance 1824, p. 306, pl. 80, figs. 3, 3*a*.

Cyrtina lapidea sp. nov.

Plate 35, figs. 11–17; Plate 36, fig. 6; text-fig. 1*a–m*

1950 *Cyrtina* sp. Warren and Stelck, p. 69.

1959 *Cyrtina* sp. Pedder, p. 472.

Ncmz derivation. Latin, *lapideus* = made of stone.

Types. Holotype, specimen originally Triad Oil Co. Ltd. collection no. X461, now Geological Survey

of Canada type no. 14,614. Three preserved paratypes, specimens originally Triad Oil Co. Ltd. collection nos. X46m-0, now Geological Survey of Canada type nos. 14,125 to 14,617. Fourth paratype, specimen originally Triad Oil Co. Ltd. collection no. X46p, subsequently destroyed for serial sectioning.

Type stratum. Hay River formation coquina bed 630 feet below top (Crickmay 1957, p. 6; not 1953 p. 11); Upper Devonian, Frasnian.

Type locality. Canada, North West Territories, Hay River opposite mile 14 of the Mackenzie Highway (Grimshaw Road) measured south-westward, about 80 feet above water-level and 10 feet below bank top. Latitude $60^{\circ} 41' N.$, longitude $115^{\circ} 54' W.$

Description. Shell small, subpyramidal, generally slightly asymmetrical rarely strongly asymmetrical or symmetrical. Profile subtriangular. Outline nearly semicircular. Hinge-line 95–100 per cent. of total shell width, just flexed centrally. Cardinal extremities abruptly rounded or minutely mucronate. Anterior commissure uniplicate. Shell substance moderately thick, calcitic, finely and closely endopunctate.

Pedicle valve subpyramidal, weakly convex along posterior midline, almost straight, but steeply inclined anteriorly; lateral slopes only very gently convex but steeply inclined. Sulcus with origin at beak, shallow, gently concave transversely, produced to a short semicircular tongue. Umbonal region not differentiated. Beak blunt, just projecting, straight. Beak ridges variable, either sharp or rounded. Interarea equilaterally triangular, orthoclinal, or proclinal and plane surfaced towards hinge, apsaclinal and concave towards beak, apical angle about 90° . Delthyrium with an apical angle of about 26° , closed near hinge by an arched pseudodeltidium. Foramen triangular towards beak, semi-elliptical towards pseudodeltidium, long axis four-fifths of the length of the delthyrium. Hinge teeth tear-shaped in section, of moderate size. Dental plates ankylosed to median septum in posterior 1.5 mm., of valve, withdrawn forming a spondylium from 1.5 to 3.2 mm. from beak tip, gradually reduced anteriorly, disappearing about 5.7 mm. from beak tip. Median septum high and produced to a tichorhinum in posterior 3.2 mm., gradually reduced anteriorly. Muscle scars not seen in primary material.

Brachial valve weakly convex. Fold transversely convex posteriorly, flat-topped anteriorly, low, elevated only in anterior three-fifths of adult valve. Umbonal region and beak not differentiated. Interarea linear. Hinge-plate well developed about the sockets and socket plates, divided by a median ridge. Sockets large, bounded internally by, and partly excavated into, strong socket plates, divergent to each other at 90° . Cardinal process bilobed, smooth. Spiralia not preserved in primary material, attachment confluent with the anterior parts of both the socket and hinge plates. Median septum extremely low and fine, absent in anterior two-fifths of valve.

Ornamented by from 5 to 8, typically 7, costae on the pedicle valve and by from 4 to 7, typically 6, on the brachial valve; costae rounded and progressively diminished laterally. Sulcus smooth. Fold smooth or with very weak anterior median furrow. Interarea with vertical striae. Growth lines irregular, mostly very fine and crowded, especially on the interarea, but gerontic specimens may bear coarser growth lines near the commissure. Abundant fine endopunctae clearly visible on shell surface, except on the interarea.

Dimensions. Holotypes and paratypes 1 to 3, length 4.7, 5.3, 5.2, and 6.4 mm., width 7.7, 7.0, 6.6, and 8.0 mm., depth 5.4, 5.1 (both valves), 1.1 and 1.8 (brachial valves only) mm.

Distinctions. From *C. inulta* Stainbrook, occurring in the Independence formation of Iowa, this species is distinguished by its smaller ($\times \frac{2}{3}$) average size, finer costae, less

developed sulcus and tongue and by the absence of a micro-ornament of fine radial granulate ridges described on *C. inulta*. The internal structure of *C. inulta* is undescribed in literature; there may be, therefore, further distinctions between the two species.

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THE DOWNTONIAN OSTRACODERM *CORVASPIS* *KINGI* WOODWARD, WITH NOTES ON THE DEVELOPMENT OF DERMAL PLATES IN THE HETEROSTRACI

by L. B. TARLO

ABSTRACT. Further specimens of the Downtonian Ostracoderm *Corvaspis kingi* Woodward are described, and the genus is shown to belong to the family Psammosteidae. The variation of ornamentation seen in *Corvaspis* is used to demonstrate the relationship between the three main types of growth of dermal plates known in the Heterostraci.

INTRODUCTION

THE affinities of the ostracoderm *Corvaspis kingi* have been the subject of much debate, but the discovery of new material and a reinterpretation of that already known now make it possible to place the genus in the family Psammosteidae, so that the family Corvaspidae becomes redundant.

A fragment of this ostracoderm, which had been collected by Professor J. Kiaer from the Downtonian of Spitsbergen, was figured although not described, by Jaeckel (1927, p. 925) as a new Palaeaspid (Cyathaspid). Woodward (1934, pp. 566–7) erected *Corvaspis kingi* for similar material from the Downtonian of Corvedale (Shropshire) collected by Mr. W. W. King, and placed the genus in the Cyathaspidae. Stensiö (1944, p. 4) recorded *Corvaspis* from the Czortkow Series of Podolia.

Denison (1953, pp. 304–18) redescribed the unusual ostracoderm *Cardipeltis* and noted that its histological structure and ornamentation closely resembled those of *Corvaspis*, but as little was then known of *Corvaspis* he was unable to suggest the possible relationship between these two genera. A few months after Denison's paper appeared, Dineley (1953) described further remains of *Corvaspis* including median plates, ridge plates, and orbital plates, as well as small irregular plates and scales.

Corvaspis, like most Heterostracans, has a complex carapace of bony plates covering its head and the anterior part of its trunk, the posterior part being covered by small scales. The carapace is made up of a number of different plates, the presence or absence of which is of diagnostic value. Dineley showed that *Corvaspis* must be excluded from the Cyathaspidae since it possesses orbital plates; he also regarded it as having ridge plates, and although he considered that the genus might be 'akin to the Drepanaspidae' (Psammosteidae), an animal having ridge plates clearly did not belong to any known family (1953, p. 166). In consequence, he felt justified in proposing a new family—the Corvaspidae—to receive *Corvaspis kingi* and his new species *C. graticulata*. As is shown below, however, Dineley's so-called 'ridge plates' can better be interpreted as branchial plates, thus equating *Corvaspis* with most other Heterostracans, and removing the necessity for a separate family.

Bystrow (1955, pp. 472–523) figured the microstructure of *Corvaspis kingi* which appears Cyathaspid in nature, but he showed that it was similar in certain respects to

Kallostrakon podura which in turn could be compared with the Psammosteid *Psammolepis paradoxa*. Recently Stensiö (1958, pp. 321–6) reviewed previous work on *Corvaspis*, retaining it in the order Corvaspida (= Corvaspidae of Dineley). At the same time he suggested that the Ludlovian *Strosipherus* and the Dittonian *Penygaspis* might be included in this order. Further specimens of *Corvaspis kingi* collected during 1953–5 by Mr. J. R. L. Allen, Dr. L. G. Love, Dr. T. Orvig, Mr. H. A. Toombs, and myself are described below, and these help to establish the Psammosteid affinities of the genus. The new material comes from the Earnstrey Hall locality in Shropshire, details of which can be found in Wills (1935, p. 427). Most of the specimens come from the ‘4-foot band of very tough calcareous pellet rock and conglomerate’, a large block of which has fallen into the bed of the stream.

DESCRIPTION OF PLATES

Median plates. Dineley (1953, p. 171) described an almost complete median plate, which Stensiö (1958, p. 324) suggests was on the ventral surface of the body. This plate is somewhat oval in outline, its anterior border being gently curved while the lateral borders are more or less straight. Unfortunately the posterior border is missing. The new material contains a complete median plate which has a similar anterior border, and a posterior border which is almost straight transversely. Its lateral edges are also fairly straight, but they tend to diverge posteriorly, so that, as can be seen from text-fig. 1, the plate is narrower anteriorly. A small plate is incorporated within the median plate on one side of the posterior part, making it asymmetrical.

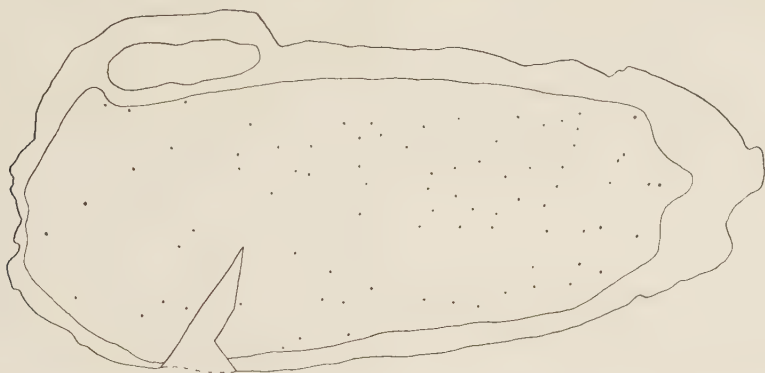
There are other ventral median plates which seem to be variations on the simple oval one already described. In these the central part of the anterior border is produced, as shown in text-fig. 2*b*.

The type specimen described by Woodward is the anterior part of a median plate, the anterior border of which is deeply excavated at the midline. Stensiö interprets this plate as forming part of the dorsal surface of the animal, and the new collection also includes a similar bilobed median plate (see Pl. 38, fig. 3). In the Psammosteids, the Pteraspids, and also the Traquairaspids, the dorsal median plate has an excavated anterior border, while the border of the ventral plate is generally convex, thus *Corvaspis* may well be related to one of these groups.

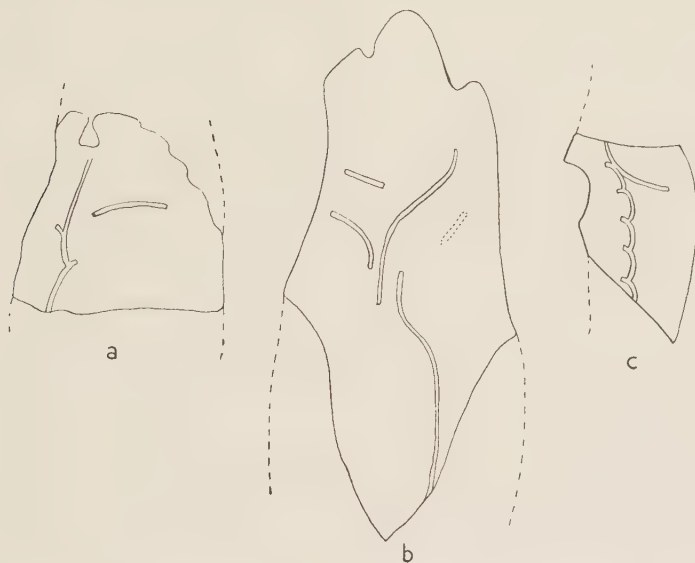
Both Woodward and Dineley noted that the sensory pores were in two irregular lines running longitudinally on either side of the median plates, and in text-fig. 1 the complete median plate is shown with the pores plotted. Though this gives some indication of the pattern of the sensory canal system itself, it can only be fully ascertained by grinding the specimen through to just below the dentine layer where the canal system properly occurs. This has recently been attempted, and from the specimens figured below (text-fig. 2) it appears that the canal system found is roughly comparable to those known in other Heterostracans, although the pattern is not a clear-cut one and cannot be used with any certainty. When more specimens are available to allow the necessary sacrifice, it may be possible to obtain a complete picture of the canal system in *Corvaspis*.

The ornamentation of the dermal plates is quite distinctive and can readily be used to identify the genus. Generally it consists of flat-topped dentine ridges with a faintly crenulate base; these ridges are usually disposed longitudinally and, as noted by Woodward (1934), in the median plates ‘an irregular network of fine grooves divides this ridge

ornament into small areas which have the false appearance of separate plates'. Woodward also described an ornamentation in which these small polygonal areas were separated by rows of small rounded tubercles instead of faint grooves and, as noted by Dineley, both types of ornament can appear in one plate. Stensiö (1958, p. 324) suggested



TEXT-FIG. 1. *Corvaspis kingi* Woodward. Ventral median plate with sensory pores plotted, wide border of rounded tubercles indicated; isolated area in upper left portion of figure represents incorporated tesserae. $\times 1$, B.M. P.40575.



TEXT-FIG. 2. *Corvaspis kingi*. Fragments of median plates showing sensory canals; all horizontal sections taken at junction of cancellor layer and outer dentine layer. *a*, $\times 1$, A-T 225; *b*, Anterior part of ventral median plate. $\times 1$, A-T 238; *c*, $\times 1$, A-T 309.

that the polygonal areas separated by tubercles belonged to the posterior part of the plate, the others being anterior. Some of the median plates recently found show that in *Corvaspis* there is a much greater variety of ornament than was formerly realized. It is in fact possible to trace a gradation from an ornamentation of polygonal areas separated

by tubercles to one in which the longitudinal dentine ridges continue almost the whole length of the plate without a break. The significance of this variation is discussed below. In addition all median plates, whatever their form of ornamentation, have a wide border of rounded tubercles.

A specimen is also figured (Pl. 38, fig. 6) which shows the healing of damage in the carapace, the area of new growth consisting of dentine ridges arranged in random fashion.

Branchial plates. Some arched, elongate, asymmetrical plates were termed 'ridge plates' by Dineley (1953, p. 174), since he believed that they might correspond to the 'ridge scales' (fulcral scales) of other Heterostracans. He suggested that their degree of arching



TEXT-FIG. 3. *Corvaspis kingi*. Left branchial plate, showing asymmetry and flange with broad notch on upper part of figure. $\times 1\frac{1}{2}$, A-T 233.

indicated that they were placed in the median line of the trunk or tail region rather than in a lateral position. The plate he figured is incomplete along one border, but luckily one of the new specimens is complete in this region and shows that the plate is even more asymmetrical than Dineley suspected; one border, probably the dorsal, having a very distinctive broad notch (see text-fig. 3). The arching and general shape of the plate is similar to that seen in the branchial plates of

the Cyathaspids, Pteraspids, and Traquairaspids, and this, coupled with the strong asymmetry, suggests that the plate is in fact a branchial. Moreover, the specimen figured by Dineley shows a sensory canal running obliquely across one corner, which is consistent with its being a branchial plate rather than a ridge plate.

Along the crest of the branchial plate is a line of small tubercles, around which the adjacent dentine ridges curve, giving a very characteristic pattern. The remainder of the plate is covered with short ridges aligned longitudinally, except where they curve round the sensory pores.

Orbital plates. Dineley (1953, p. 173) described and figured orbital plates for the first time, although all his specimens were small with irregular margins. Subsequently a specimen was discovered which shows that the orbitals are large rectangular plates with a circum-orbital sensory canal (Pl. 37, fig. 2). The specimens figured previously would thus seem to have been merely the central portions of the orbital plates, and this new find is of some significance since such a large orbital plate can only be envisaged as belonging to the carapace of a dorso-ventrally compressed animal like a Psammosteid. Previously the orbitals were taken to be small plates, which might well have belonged to any Heterostracan family outside the Cyathaspids.

In the central portion of the orbital plate, the dentine ridges are arranged in concentric rows around the orbital cavity, the rest of the plate being composed of a wide border of small tubercles. In one sector, however, the dentine ridges form a series of concentric rings around sensory pores.

Lateral plates. Dineley's small irregular plates are of two kinds: first those similar to the plate incorporated in the median plate described above, which are here termed tesserae, and second those here regarded as lateral plates. The latter, unlike the tesserae, have

their dentine ridges arranged in a haphazard manner; some have a rather intricate outline, whereas others with a more simple outline are traversed by sensory canals (Pl. 37, figs. 5, 6). These lateral plates probably occur in the pre-orbital region of the ventral surface, situated behind and to the side of the mouth.

Tesserae. It was suggested by Dineley that the median plate was surrounded by a mosaic of small plates, and this is confirmed by the fact that they may become incorporated into the median plate around its margin (Pl. 37, fig. 1). Such fields of tesserae between the major plates are characteristic of the Psammosteidae. Unlike the lateral plates the tesserae are fairly simple in outline and in some the ornamentation consists of small tubercles arranged concentrically; others have a pattern of longitudinal ridges with only a narrow border of tubercles (Pl. 37, figs. 3, 4).

Post-orbital plate. A single asymmetrical and somewhat arcuate plate is included in the new collection (Pl. 37, fig. 7). It seems unlikely that this plate could have occupied a median position in the body and it is tentatively suggested that it represents a post-orbital plate, such as is present in the Psammosteids.

Microstructure. The histological structure of the plates and scales of *Corvaspis kingi* has been described and figured by Bystrow (1955, pp. 492–4). However, under high magnification it can be seen that the normal dentine tubules rebranch into innumerable and much finer tubules which continue through the seemingly structureless outermost layer to the exterior, as is shown in Pl. 37, fig. 8b.

AFFINITIES OF *CORVASPIS*

As has been demonstrated the possession of orbital plates excludes *Corvaspis* from the Cyathaspididae despite the fact that its plates have a similar histological structure, the cancellar layer possessing large spaces which reach from the basal lamellar layer to the outer dentine one. Moreover, it possesses fields of tesserae which are known only in the Ordovician Astraspidids and the Psammosteids, but it is excluded from the former by its histological structure. This suggests Psammosteid affinities for *Corvaspis* but in the Psammosteids the cancellar layer has a spongy appearance. However, a transition from the typical Psammosteid condition to that in *Corvaspis* can be seen in *Kallostrakon podura* Lankester (a form related to *Corvaspis*) where both spongy tissue and large spaces are present.

The large flat orbital plates fit best into the structure of a dorso-ventrally compressed animal such as the Psammosteid *Drepanaspis* (Obruchev 1943, pp. 268–71), and the plate interpreted as a post-orbital, if correctly diagnosed, would mean that *Corvaspis* must belong to this family since only in the Psammosteids is such a plate known.

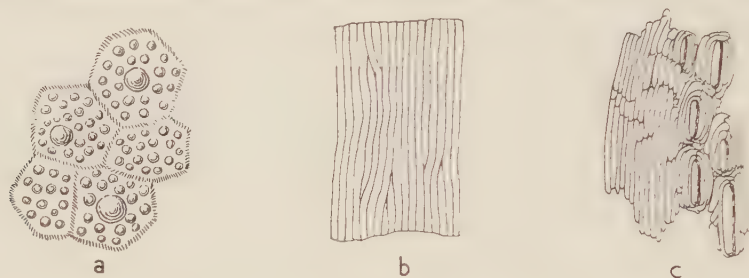
The evidence thus points to the Psammosteid affinities of *Corvaspis* and for this reason it is here included within the family Psammosteidae, making it no longer necessary to retain the family Corvaspididae.

As noted above, the Dittonian *Cardipeltis* is similar to *Corvaspis* in both its histology and ornamentation, and in the possession of tesserae, branchials, and median plates. However, in *Cardipeltis* the median plate extends laterally as far as the branchial openings, whilst *Corvaspis* has a field of tesserae on either side of the median plate. If, in *Corvaspis*, the fields of tesserae around the median plate were to be completely incor-

porated into it, then a median plate similar to that in *Cardipeltis* could be produced. From the pattern of the sensory canal system in *Cardipeltis* it is clear that the known median plates extend only as far as the pineal region, and it seems reasonable to assume, as Stensiö has done (1958, p. 328), that there were small plates and orbitals anterior to the median plates. If this were so and further fusion of plates took place, one would have the condition where an entire carapace could arise as a single unit. This occurs in the Emsian Amphiaspids described by Obruchev (1938; 1958) from north-west Siberia, and *Cardipeltis* could thus be interpreted as an early offshoot from the Psammosteid stock leading to the Amphiaspids.

DEVELOPMENT OF DERMAL PLATES IN THE HETEROSTRACI

After the discovery by Woodward and White (1938) that primitive Elasmobranch scales are composite in nature, Orvig (1951) and Stensiö (1958) developed a new theory on the growth of scales and dermal bone in the lower vertebrates. Their recognition of



TEXT-FIG. 4. Ornamentation of dermal plates. *a*, *Astraspis* sp., showing independent polygonal tesserae and zones of tubercles produced by cyclomorial growth. *b*, *Poraspis* sp., showing longitudinal dentine ridges produced synchronomorially. *c*, *Tolepelepis* sp., showing individual units produced by cyclomorial growth, with adjacent synchronomorial area.

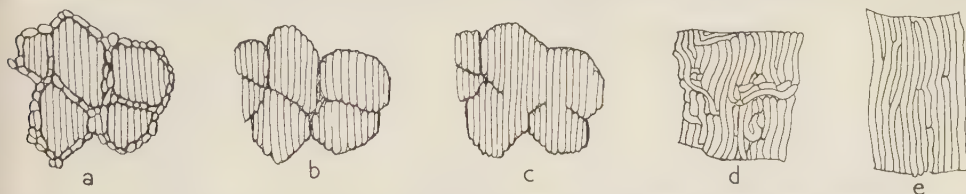
the fact that two types of growth occur in dermal plates is here used to assess the significance of the variation in ornamentation within the Heterostraci.

The most primitive Heterostraci known are the Ordovician *Astraspidae*, which have a carapace composed of isolated polygonal tesserae. These small plates have an ornamentation consisting of one large tubercle surrounded by concentric rows of smaller tubercles. It is evident that during the early stages of ontogeny, single isolated tubercles were present in the skin which formed primordia around which successive zones of tubercles appeared, until the animal reached its definitive size, when the borders of the small plates thus formed would meet. The growth of these individual units by addition of zones of tubercles is termed cyclomorial growth by Orvig (1951, p. 367) (see text-fig. 4a).

In Silurian times the Heterostraci were represented by the *Cyathaspids* which had a carapace composed of two median plates and two branchials. These plates are ornamented by longitudinal dentine ridges, and in general appeared only when the animal was fully grown. There are no signs of cyclomorial growth, each plate being formed as a complete unit, with the dentine ridges all appearing simultaneously. This type of growth Orvig (1951, p. 367) termed synchronomorial (see text-fig. 4b).

A number of *Cyathaspids* are known from the Ludlovian of Oesel which do not possess this general type of ornamentation, but instead have one which can easily be

derived from that seen in the Astraspids. The dorsal plate in *Tolepelepis*, for example, is made up of many cyclomorior elements, in each of which there is a longitudinal primordium, with smaller longitudinal ridges on either side. In the posterior part of the plate these elements take on the appearance of imbricating scales. The lateral region of the dorsal plate of *Tolepelepis*, however, has a similar ornamentation to that of the more normal Cyathaspids, showing synchronomorior growth, the only vestige of the individual elements being the faint grooves which break up the longitudinal dentine ridges (see text-fig. 4c). *Corvaspis* from the Downtonian shows further stages in the growth of the dermal plates, its median plates being more advanced than those of *Tolepelepis*. In *Corvaspis* the plates also appear to be formed of numerous polygonal units fused together, but each unit is formed synchronomoriorally in contrast to the cyclomorior formation in *Tolepelepis*. In the posterior part of the median plates of *Corvaspis*, the synchronomorior units are separated from one another by narrow zones of tubercles



TEXT-FIG. 5. Variation of ornament in *Corvaspis kingi*. *a*, Polygonal synchronomorior units with margins of tubercles produced by cyclomorior growth. *b*, Polygonal synchronomorior units separated by grooves. *c*, Partial fusion of adjoining synchronomorior units. *d*, Complete fusion of original polygonal units giving single large synchronomorior area with occasional random ornamentation. *e*, Final stage showing longitudinal dentine ridges running almost without a break (cf. *Poraspis* fig. 4b).

formed cyclomoriorally, giving the units the appearance of scales (Pl. 38, fig. 1; text-fig. 5a). It seems likely that, as suggested by Stensiö, the median plates gradually became continuous in this way with the squamation of the scales.

Normally the polygonal units are marked off from one another by faint grooves (Pl. 38, fig. 2; text-fig. 5b), but in some cases this division into individual units is incomplete, the dentine ridges of two or three synchronomorior units being continuous, probably due to the units fusing before calcification (Pl. 38, fig. 3; text-fig. 5c). A further stage is well seen in Pl. 38, fig. 4, and text-fig. 5d, where the only trace of the original polygonal unit is an occasional faint transverse groove and an irregularity in the arrangement of the dentine ridges. This type of ornament is also seen in the Dittonian *Cardipeltis* which seems to suggest that this genus is a direct descendant of *Corvaspis*. The final stage in the trend of ornamentation is seen in a specimen of *Corvaspis* in the collection of Birmingham University (B.U. 717) which shows a median plate ornamented by straight longitudinal ridges, which extend almost the whole length of the plate without interruption (Pl. 38, fig. 5; text-fig. 5e).

A similar trend is seen in *Traquairaspis* (Pl. 38, fig. 7) where the primitive Downtonian *T. campbelli* has, in the centre of the ventral median plate, a large synchronomorior unit in which the ornamentation is random as in *Corvaspis* (text-fig. 5d), suggesting that it was derived from a number of small individual units. The later Downtonian *Traquairaspis symondsii* possesses a large central synchronomorior unit completely devoid of ornamentation (White 1946). In both cases the central unit has around it concentric zones of cyclomorior growth.

In *Corvaspis* also, whatever the form of ornamentation of the median plates, they are bordered by rows of small rounded tubercles forming a zone of cyclomorior growth. This type of median plate in which there is a large central synchronomorior unit around which there is an area of cyclomorior growth is also seen in the primitive Dittonian Pteraspid *Penygaspis dixonii* (White), although in this case the ornamentation is typically Pteraspid (White 1938; Stensiö 1958) (text-fig. 6).

If the synchronomorior unit were acquired early in the ontogeny instead of when the animal was approaching its definitive size, and the area of its median plates continued to increase by concentric growth, this would give the normal type of growth seen in the Pteraspids, which are an advanced group of the Heterostraci. That this is more likely than the evolution of the Pteraspid type of growth direct from the Astraspid condition is borne out by vestiges of the primitive condition found in some Pteraspids. *Pteraspis althi* Stensiö, for example, has a pre-oral region composed of small polygonal synchronomorior units rather like those seen in *Corvaspis* (Stensiö 1958, p. 277) while in *Rhinopteraspis dunensis* (Roemer) this same region is composed of a single synchronomorior unit in which the dentine ridges run longitudinally without a break (Tarlo 1958). These contrast with *Pseudopteraspis elongata* (Zych), which has the normal Pteraspid cyclomorior growth in its pre-oral region, and as figured below (text-fig. 7) these examples of fundamentally different Pteraspids demonstrate the



TEXT-FIG. 6. *Penygaspis dixonii* (White), showing large central synchronomorior unit around which concentric growth occurs cyclomoriorially (after White 1938).

three main types of ornamentation found in the Heterostraci.

EXPLANATION OF PLATE 37

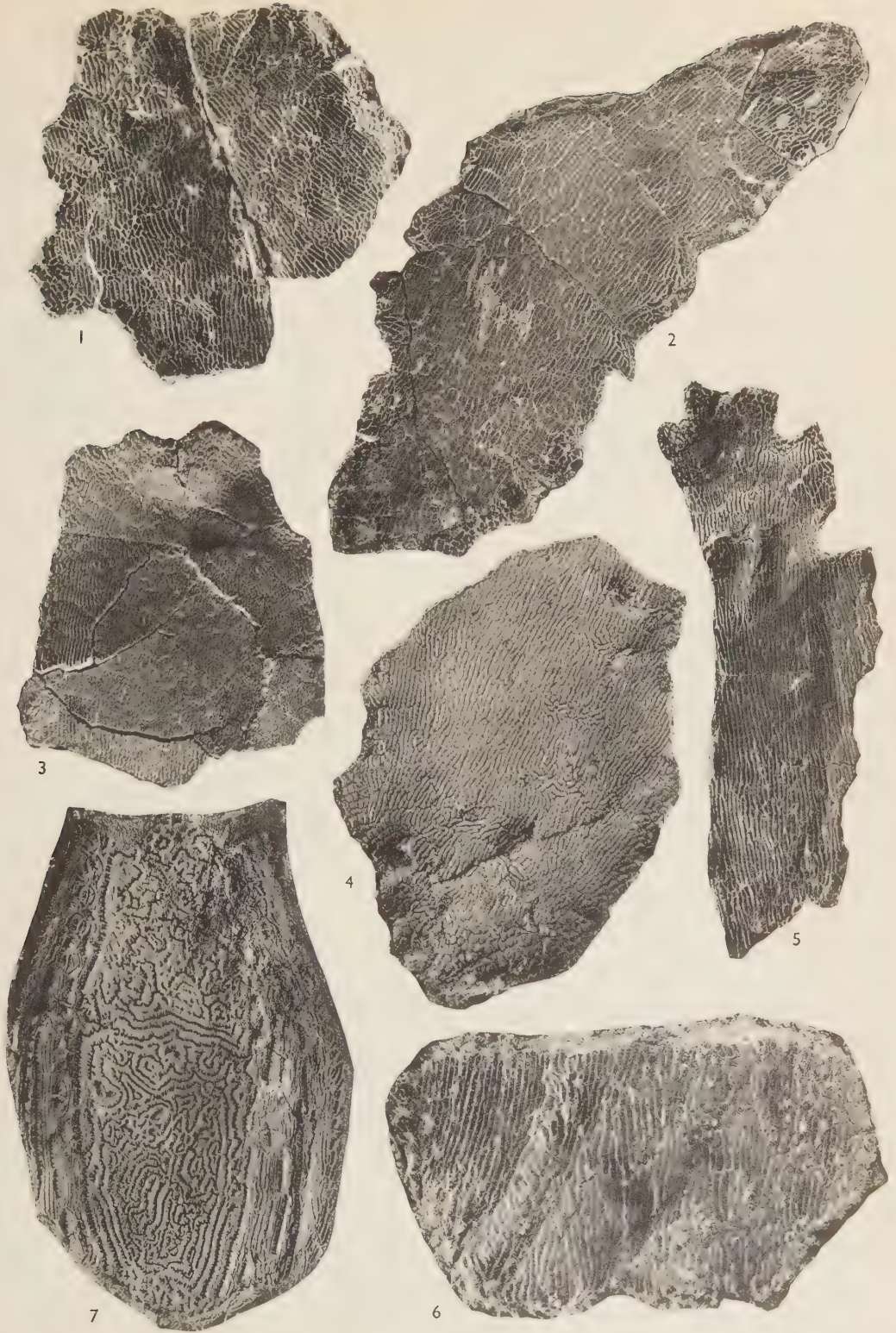
Figs. 1-8. *Corvaspis kingi* Woodward, Downtonian, Earnstrey Hall, Shropshire. 1, Anterior part of ventral median plate, showing the incorporation of tesseræ on one side. $\times 2$, B.M. P.40573. 2, Orbital plate. $\times 3$, A-T 231. 3, Tessera, showing cyclomorior growth. $\times 3$, A-T 308. 4, Tessera, showing synchronomorior growth. $\times 3$, A-T 235. 5, Lateral plate, showing haphazard arrangement of ornament. $\times 3$, A-T 234. 6, Lateral plate, traversed by line of sensory pores. $\times 3$, A-T 226. 7, ?Post-orbital plate. $\times 2$, B.M. P.40574. 8a-b, vertical section of scale. A-T 206. 8a, Complete scale. $\times 40$. 8b, Part of scale, showing fine dentine tubules in outermost layer. $\times 220$.

EXPLANATION OF PLATE 38

Figs. 1-6. *Corvaspis kingi* Woodward, Downtonian, Earnstrey Hall, Shropshire. 1, Fragment of median plate, showing polygonal areas separated by tubercles. $\times 2$, B.U. 718. 2, Ventral median plate, showing polygonal areas separated by faint grooves. $\times 2$, A-T 236. 3, Dorsal median plate, showing fusion of polygonal areas. $\times 2$, A-T 237. 4, Ventral median plate, showing areas of random ornamentation. $\times 2$, A-T 201. 5, Fragment of median plate with little trace of polygonal areas. $\times 2$, B.U. 717. 6, Fragment of median plate showing healed area with random ornamentation. $\times 3$, B.M. P.17038.

Fig. 7. *Traquairaspis campbelli* (Traquair), Downtonian. Natural mould of ventral median plate, showing central synchronomorior unit with random ornamentation, with outer zone of cyclomorior growth. $\times 2$, B.M. P.27380.





Thus it can be seen that what were formerly considered to be three distinct types of growth of dermal plates in the Heterostraci are all related. The most primitive type is that in which independent cyclomorioral plates increase in size until they form a complete trapace; the next major stage is where the complete median plate is a single synchro-morioral unit, and finally if this unit is acquired at an early stage of life it can become a primordium around which cyclomorioral growth can occur until the animal is fully developed.

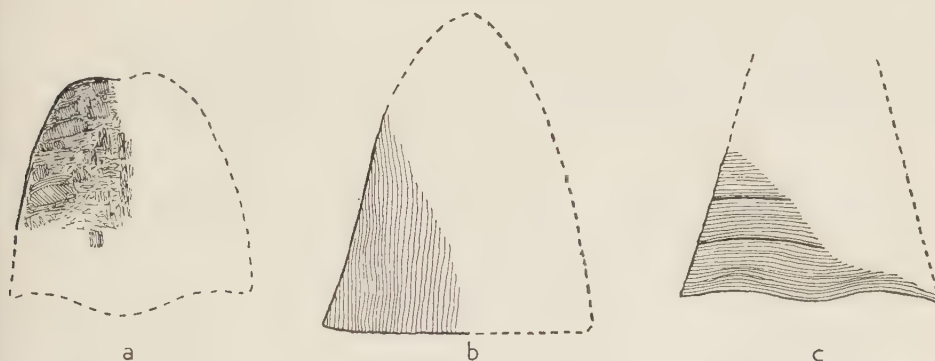


FIG. 7. Ornamentation of pre-oral regions in the pteraspids. *a*, *Pteraspis althi* Stensiö, showing individual synchronomorioral units. *b*, *Rhinopteraspis dunensis* (Roemer), showing large single synchro-morioral unit. *c*, *Pseudopteraspis elongata* (Zych), showing zones of cyclomorioral growth.

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Repositories. A-T., Allen-Tarlo Collection, Reading University; B.U., Geological Department, Birmingham University; B.M., British Museum (Natural History), London.

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AUSTRALOSUTURA GEN. NOV. (TRILOBITA) FROM THE CARBONIFEROUS OF AUSTRALIA AND ARGENTINA

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ABSTRACT. A revised description of the Carboniferous trilobite *Cordania gardneri* Mitchell 1922 is given, based on some topotype material from Australia, and new material from Argentina. The species is assigned to a new genus *Australosutura* Campbell and Goldring 1960.

LOCATION AND STRATIGRAPHY OF MATERIAL FROM AUSTRALIA

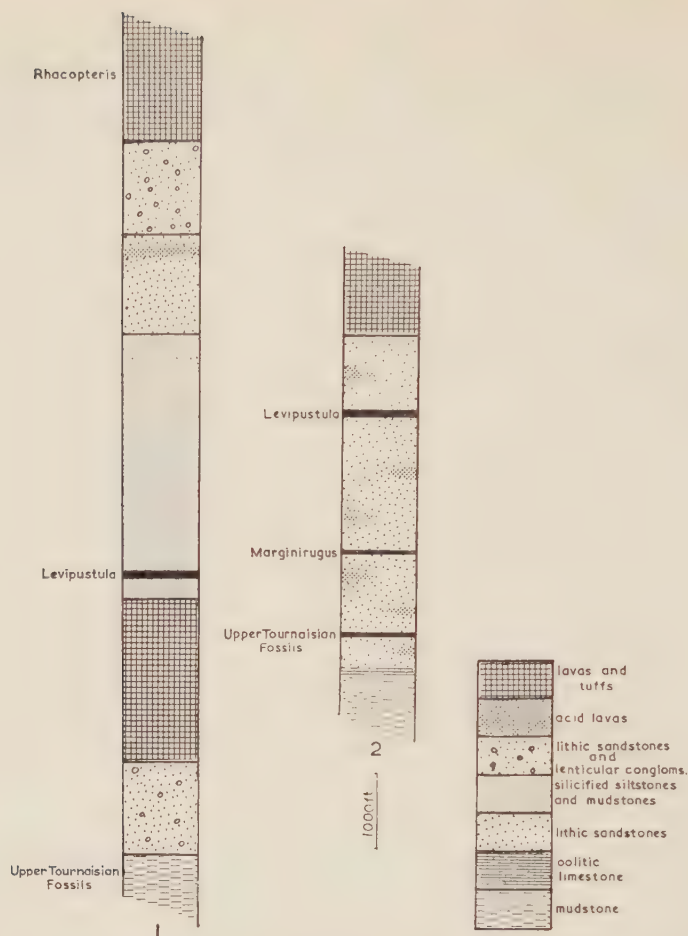
Australosutura gardneri was first described by Mitchell (1922, p. 536) from the shore of Lake Boolambayt, one of the Myall lakes north of Newcastle, New South Wales. The stratigraphy of this area is still poorly known, though it is being studied at the present time. The specimens of *A. gardneri* occur in a richly fossiliferous bed an unknown interval (some hundreds of feet at least) above a very prominent sandstone containing the brachiopod *Marginirugus barringtonensis alatus* Campbell 1956, which is considered to be of Lower Viséan age. Fortunately the species is known from two other New South Wales localities where the stratigraphy has been more adequately studied; the Barrington area (Voisey 1940), and the Booral area (Osborne 1950); the successions in these areas have been re-examined recently, and the results are set out in the accompanying columns (text-fig. 1).

In all three areas *A. gardneri* is associated with a very distinctive fauna dominated by the productid *Levipustula* Maxwell 1957 and an undescribed acrospiriferid. However, though all three faunas have many elements in common and are quite distinct even at the generic level from the earlier Carboniferous faunas, they are not identical, and it is possible that they are only approximately contemporaneous.

The *Levipustula* fauna is also very prominent in Queensland where it occurs extensively in the Neerkol mudstones which overlie the late Viséan limestones of the Rockhampton Series of the Rockhampton area, and the Turner Creek Clastics of the Mt. Morgan area, the upper parts of which are Viséan (Hill 1934; Maxwell 1954). The Neerkol mudstones are generally considered by Queensland geologists to be of Muscovian age. Study of the brachiopods, bryozoa, and molluscs of the *Levipustula* faunas of the three New South Wales localities indicates a Westphalian age and hence broadly confirms the Queensland determination. A systematic study of the fauna is to be published shortly.

The most significant fossils for the determination of age are: Spirifers similar to the Pennsylvanian *Neospirifer triplicatus* (Hall); *Lissochonetes*, which is known only from post-Viséan deposits elsewhere; *Levipustula*, which is common in the Westphalian of western Europe, but is not yet known from elsewhere; *Limipecten*, which, although it is known from the Viséan of western Europe, does not appear until the Upper Carboniferous elsewhere in the world. None of the associated fifteen genera of fossils, many of them endemic, suggests an earlier age.

K. S. W. C.



TEXT-FIG. 1. (1) Generalized stratigraphic succession east of the township of Booral on the south-eastern side of the Gloucester trough, New South Wales. (2) Generalized stratigraphic succession between Barrington and the Gloucester River, on the north-eastern side of the Gloucester trough, New South Wales.

LOCATION AND STRATIGRAPHY OF MATERIAL FROM ARGENTINA

The specimens from Argentina came from three localities in the west of the Province of Chubut: (1) La Carlota, about 8 km. south-east of Tecka, (2) Cerro Mina, east of Sierra de Languineo and 75 km. east of Tecka, and (3) Sierra de Tepuel, about 25 km. south of Tecka. At these three localities the trilobites were found in silicious nodules at the top of the lower section of the 5,200 m. of Upper Palaeozoic sediments exposed at the Sierra de Tepuel, Sierra de Languineo, and Sierra de Tecka of Suero's (1948, 1950) 'Tepuel System'.

The lower section, 3,200 m. thick, consists of glaci-marine conglomerates together with sandstones, quartzites, and greywackes with intercalated shales. The upper section

,000 m. thick, differs from the lower by the absence of glacial conglomerates and grey-slates, but includes micaceous sandstones and shales with well-preserved plant remains. The lower section has yielded brachiopods, pelecypods, bryozoans, gastropods, conulariids, corals, and fish scales. The upper section has also yielded brachiopods including *Levipustula*, and the brachiopods from both sections are now being studied (Amos, in press). In the upper section goniatites have been found. Miller and Garner (1953, p. 821) described *Anthracoceras? argentinense* Miller and Garner 1953 and *Eoasianites sp. 4? argentinense*, although found at La Carlota together with the trilobites, was not found *in situ* but came from a pebble of dark limestone. Curiously no limestone beds are exposed in the neighbourhood and possibly the pebble came from a bed no longer exposed. Miller and Garner gave the age of the goniatites as Middle Pennsylvanian (Westphalian). Amos considers the age of the lower section to be Viséan on brachiopod evidence.

A. J. A.

DESCRIPTION

Family BRACHYMETOPIDAE Prantl and Přibyl 1950 emended Hupé 1955

AUSTRALOSUTURA gen. nov.

Type species *Cordania gardneri* Mitchell 1922

Derivation of name. From the southern hemisphere, and with facial sutures.

Range. Carboniferous. The age of the beds in which the trilobites occur is not known with certainty either in New South Wales or in Argentina. Although it is suggested that the age of the beds in Argentina is Viséan it is thought that the age of the beds in Australia is Westphalian. Further research may produce more conclusive data for the age determination in both countries.

Distribution. New South Wales, Burindi, and Kuttung Series; Argentina, top of lower section of 'Tepuel System'.

Diagnosis. Cephalon and glabella strongly inflated. Glabella subcylindrical with prominent, subtriangular basal lobes and deep glabellar furrows 1p. Glabellar furrows 2p clear. Preglabellar field short and high. Very broad, concave, and pitted border furrow preceded by short convex border. Sublunate, strongly convex eyes. Long genal spines. Facial suture curves strongly away from eye. β on crest of border and ω just inside genal spines. Surface of cheek area, preglabellar field, glabella and occipital ring with numerous tubercles. Thorax of nine tuberculate segments. Pygidium with fifteen rings and nine (+1-2) ribs. Axis semioctagonal in cross-section, and overhanging postaxial portion, but not border. Rings strongly arched and tuberculate with prominent median row. Ribs with anterior portions twice as strong as posterior portions and both tuberculate.

Comparisons with other genera. Mitchell (1922, p. 537) concluded that *A. gardneri* could not be included in either *Phillipsia* Portlock 1843 or *Griffithides* Portlock 1843. He commented on its very close similarity to species of *Brachymetopus* M'Coy 1847, but decided that the presence of facial sutures prevented its inclusion with this genus. On the suggestion of Vogdes he finally assigned the species to *Cordania* Clarke 1892.

The cephalons of *Cordania* and *Australosutura* are similar in each having a highly inflated glabella, faint glabellar furrows 2p, and prominent detached basal lobes. In *Australosutura* the glabella is relatively longer, and the preglabellar field shorter and

steeper. Both genera have nine thoracic segments. The pygidia differ considerably. In *Cordania* it is transversely elliptical; in *Australosutura* it is comparatively longer, has a greater number of rings and ribs, fifteen rings and nine (+1-2) ribs as against thirteen rings and eight ribs in *Cordania cyclurus* (Hall and Clarke 1888), and the termination of the axis overhangs the postaxial portion, though not the border. The form and surface of the rings and ribs differ; in *Cordania* the anterior and posterior portions of the ribs are about equally developed and bear granules in addition to the tubercles on the anterior portions. Both portions continue to the margin.

In much of the material from Australia and Argentina the free cheeks are attached to the cranium, and Mitchell (1922, p. 538) considered that fusion of the cheeks had begun. Whittington (personal communication) regards the facial suture of *Cordania* as normal and functional. Since isolated free cheeks and cranidia of *Australosutura* have been found in Australia the facial suture cannot be regarded as otherwise than functional. *Cordania* may possibly be ancestral to *Australosutura*.

Australosutura differs from the type species of *Brachymetopus* (type species *Phillipsia maccoyi* Portlock 1843, Goldring and Stubblefield 1957, p. 421) in possessing facial sutures, a longer glabella, and shorter preglabellar field. The details of the skeletal surface, in particular, the pair of prominent tubercles between the glabella and the anterior part of the eye, the row of tubercles on the border of the cephalon, and the tubercles on the pygidial axis, are very similar to that present in *B. maccoyi* and in *B. woodwardi* Whidborne 1896 (Goldring 1955). *B. strzeleckii* M'Coy 1847 also has similar features though the glabella is much shorter than in *A. gardneri*. In *B. uralica* d. Verneuil 1845 the anterior border is less arched than in either *A. gardneri* or *B. maccoyi*. The pygidium of *A. gardneri* is close to *B. maccoyi* and *B. uralica* though the medial tubercles of *A. gardneri* are of more even size on successive rings; the ribs of *B. woodwardi* and *B. maccoyi* are very similar to those of *A. gardneri*, but the ribs of *B. uralicus* bear a greater number of tubercles on both portions.

Australosutura gardneri (Mitchell 1922)

Plates 39, 40

1922 *Cordania gardneri*, n. sp.—Mitchell, p. 536, pl. 54, figs. 1-7.

1924 *Cordania gardneri* Mitchell—Mitchell, p. 53, pl. 10, fig. 15.

Derivation of name. After Frank Gardner who first brought the species to notice.

Lectotype. Broken cephalon figured by Mitchell (1922, pl. 54, fig. 1, Australian Museum, Sydney F.26974). Of the several specimens figured by Mitchell, those figured as pl. 54, figs. 2-5 and 7 are missing. Figure 6 of the same plate may be a reconstruction of F.27345. The specimen Mitchell figured later (1924, pl. 10, fig. 15) is F.27949.

Type locality. Brambles Farm, Myall Lakes, Eurenderee, Gloucester, New South Wales. Shore of Lake Boolambayt near grid reference 341812, Port Stephens, 1 inch: 1 mile Military Sheet.

Horizon. Upper Burindi Series (Voisey 1940, p. 196; David 1950, p. 290), Upper Kuttung Series (Osborne 1950, p. 24).

Material. Complete dorsal exoskeletons, together with independent cephalae, thoracic segments, and pygidia. No hypostomes. The material from Argentina occurs as external and internal moulds in siliceous nodules and shows little or no sign of distortion. The Australian material occurs as internal and external moulds in very fine grained sandstones and siltstones at the type locality. Specimens are

mostly distorted. The type of preservation at the other Australian localities is similar, but the sediments are coarser grained.

Diagnosis. As for the genus.

Description of material from Argentina. Cephalon. Side view. Outline of the glabella almost a quadrant, with occipital ring prominently arched, in one specimen (Museo la Plata, Coll. Suero 5024) as high as the glabella, and occipital furrow strongly rounded. Preglabellar furrow broad, shallow, and facing anteriorly. Preglabellar area short (sag.) almost vertical, bearing strong tubercles, which terminate abruptly at commencement of border furrow. The border furrow has irregularly arranged pits, of varying sizes (8–10 per sq. mm.) and is strongly concave, though the side towards the glabella is a straight slope at 45°. Border a moderately convex ridge which bears tubercles near top of posterior slope.

Front view. Occipital ring strongly arched with glabella similarly arched in front. Laterally basal lobes project beyond outline of occipital ring. Palpebral lobes slope upwards from axial furrows to prominent and strongly convex eyes. In outline posterior border of each cheek appears from behind eye and falls steeply towards genal spine. Below eye cheek descends with only slight convex slope to border furrow.

Plan. Excluding genal spines, outline of cephalon, subsemicircular, with length (sag.) rather greater than half breadth. Glabella subcylindrical, tapering anteriorly sharply between basal lobes, less so between lobes 2p and expanding very slightly beyond glabellar furrows 2p before broad, rounded termination. Basal lobes subtriangular and well defined. Glabellar furrow 1p sharp and very deep at axial furrows, becoming broad and shallow at bifurcation. Posterior branch merges into occipital furrow and anterior branch extends shortly on to glabella. Glabellar furrow 2p a broad, smooth knick, and glabellar lobe 2p only slightly inflated. No evidence from tuberculation of any more glabellar furrows. Occipital furrow deep and narrow posterior to basal lobes, expanding towards axial furrow and at junction with furrow 1p where it arches forward and becomes broad and shallow. Posterior to basal lobes, occipital ring very short (exsag.), but expanding where glabellar furrows 1p join the occipital furrow to twice this length (sag.). Small occipital node.

Area of fixed and free cheek broad. Centre of eye opposite junction of glabellar furrow 1p with axial furrow, and surrounded laterally by smooth terrace which extends to opposite glabellar furrow 2p and to half length of basal lobe. Palpebral lobe smooth. At axial furrow length of posterior border less than length of occipital ring, but border widens laterally. It is strongly convex and continues with equal prominence along genal spine. Posterior border furrow broad and smooth though narrower near axial furrow. Lateral border furrow very broad and pitted, joining posterior border furrow and continuing, with pits, down genal spine. Lateral border gently rounded, tapering gradually to base of genal spine, and then more strongly down it. Genal spine extends to fifth thoracic segment. Eye sublunate with minute facets.

Facial suture. Anterior branch curves strongly outwards, crosses border furrow and then turns inwards to margin; β at crest of border. Posterior branch curves sharply outwards and terminates only just inside base of genal spine, and rather farther from the median line than β .

Surface. Cheek area and preglabellar field with numerous close-set tubercles of variable

size (3–4 per sq. mm.), many with apical openings; one is particularly prominent on fixed cheek opposite glabellar furrow 2p. A row of slightly enlarged tubercles between palpebral lobe and axial furrow. Posterior part of fixed cheek smoother and with only a few small tubercles. Glabellar and occipital ring with tubercles of about equal size to those on cheek, but less closely spaced, and on crest of glabella very weak (on available material). Tubercles on basal lobe larger on inner part than toward axial furrow. Top of inner slope of border with a single row of tubercles which weaken laterally and are scarcely discernible along genal spine. Outer slope of lateral border and continuation of posterior border along genal spine with fine parallel terrace lines.

On ventral surface doublure, including rostrum, covered with terrace lines, and equal in breadth to border furrow plus border of dorsal surface. Facial suture continues inward course over anterior margin and meets rostral suture (rr) just below margin. There is no short connective suture but a suture (r ω), which has a course comparable to that of the perrostral suture of olenellids, makes an acute angle with the facial suture and swings outwards in a long sweeping curve to cut the posterior border of the cephalon just inside the genal spine, and immediately below the termination of the facial suture on the dorsal surface. This suture makes a definite angle with the rostral suture (rr), equal to the angle between the rostral suture and the facial suture. Inner margin of doublure (in part, presumably, hypostomal suture) long and curved, following, and lying immediately and closely under inner margin of border furrow. Doublure of free

EXPLANATION OF PLATE 39

Material from Argentina

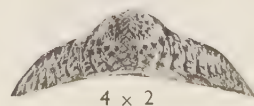
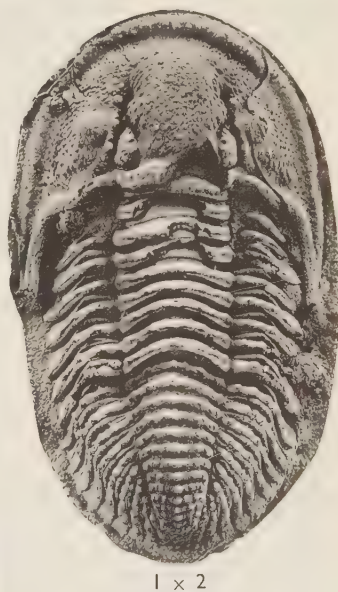
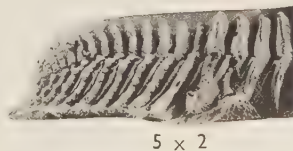
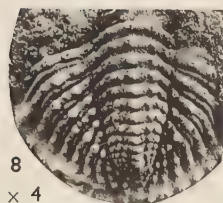
Figs. 1–11. *Australosutura gardneri* (Mitchell 1922). 1–7, Latex cast from external mould of complete specimen (BM In 53675). Province of Chubut, Sierra de Tepuel, about 25 km. south of Tecka 1, Plan, 2, front view, 3, side view of cephalon, 4, posterior view. 5, Side view of pygidium, $\times 2$. 6, Free cheek, showing puncta in border furrow, and apical openings on cheek tubercles, $\times 5$. 7, Portion showing method of articulation of segments, $\times 4$. 8, 9, Latex casts from external moulds of pygidia, Province of Chubut, La Carlota, about 8 km. south-east of Tecka. 8, $\times 4$ (Coll. Suero 5049, 5051). 9, $\times 2$ (BM In 53676). 10, 11, Latex casts from internal moulds of dorsal surface of cephalon showing rostral plate and ventral surface of free cheek, Province of Chubut, Cerro Mina, east of Sierra de Languineo, 75 km. east of Tecka, 10, $\times 2.5$ (Coll. Suero 5029), 11, $\times 2.5$ (Coll. Suero 5023).

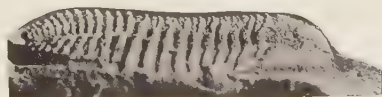
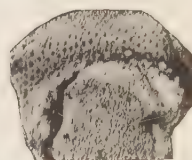
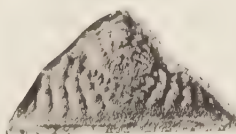
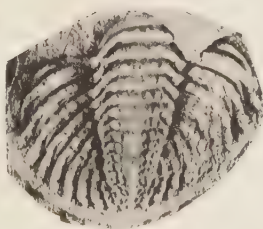
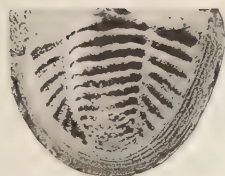
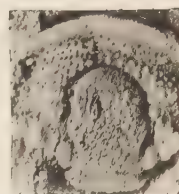
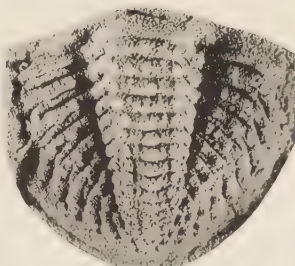
EXPLANATION OF PLATE 40

Material from Australia

All specimens are from type locality. Catalogue numbers refer to the Australian Museum Collections. Specimens figured as numbers 9, 10, 13, 14, and 15 have been destroyed by fire.

Figs. 1–20. *Australosutura gardneri* (Mitchell 1922). 1, Latex cast from internal mould of F.44640, $\times 2$. 2, 3, Dorsal and lateral views of internal mould of same specimen, $\times 2$. 4, Lectotype, F.26974, $\times 2$ (Mitchell 1922, pl. 54, fig. 1). 5, Latex cast from internal mould of free cheek, part of ventral surface of cephalon, and pygidium, F.26476c–c, $\times 2$. 6, Ventral surface of same cephalon showing position of rostrum, $\times 3$. 7, 8, Lateral and posterior views of same pygidium, $\times 2$. 9, Dorsal view of same pygidium, $\times 3$. 10, Interior view of latex cast from internal mould of cephalon, $\times 3$. 11, Interior view of latex cast from internal mould of pygidium F.26476, $\times 2$. 12, Latex cast from external mould of pygidium, $\times 3$. 13, Posterior view of latex cast from external mould of incomplete pygidium, $\times 3$. 14–16, Latex casts from external moulds of fragmentary cephalons, 14, 15, $\times 3$, 16, F.25593, $\times 2$. 17, Lateral view of latex cast from external mould of part of cephalon, showing facial suture, F.26476a, $\times 2$. 18–20, Dorsal and lateral views of internal mould, F.27949, 18, $\times 2.2$, 19, $\times 1.8$, 20, $\times 2.2$ (Mitchell 1925, pl. 10, fig. 15).





cheeks tapers very rapidly forwards, whilst rostrum broadens complementarily. There is no Panderian notch.

Hypostome. No hypostomes are present in the material from Argentina. One specimen from Australia, since lost, was figured by Mitchell (1922, pl. 54, fig. 4) but was not described.

Thorax of nine segments. Rings with strong bands which arch slightly forwards. Posterior rings slightly narrower (tr.) than those anteriorly, and outline of rings graduates from strongly rounded and close to outline of occipital ring in anterior rings, to outline of pygidial rings in posterior rings. Articulating furrow broad and shallow. Articulating half-ring as long (sag.) as ring. Rings with a weak transverse groove behind which is a very narrow posterior portion. Groove, which is finely pitted, broadens (sag.) towards axial furrow. At posterior margin of ring, at axial furrow, a deep notch. Main portion of ring with tubercles, seven prominent (+1 or 2 more), arranged in rows on successive rings; a median row and three rows on flanks. Distance between median and first lateral tubercle is $1\frac{1}{2}$ times distance between each of the three lateral tubercles. Ring process a strong node. Ventrally of articulating half-ring, front edge of each segment flexed forward to form narrow flange which runs down into ring process.

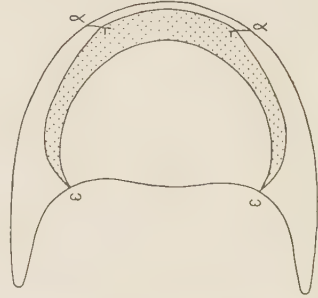
Pleurae with convex bend at fulcrum, at about one-third length (tr.). Posterior portions strongly arched (exsag.) (those on posterior pleurae more strongly so than those on anterior pleurae), narrowing at fulcrum, then broadening slightly and curving posteriorly. Posterior portions of pleurae 1-4 with slight anterior swing near margin. Laterally from fulcrum posterior portion is divided by weak furrow into anterior higher and strongly arched part and posterior lower part. At the margin anterior part rises over posterior part so that furrow faces posteriorly. Anterior parts have four to six tubercles, the one at the fulcral angle and the one between the fulcral angle and the axial furrow largest. A deep rounded furrow, which expands slightly at fulcrum, separates posterior portion of pleurae from the anterior portion, which is moderately arched on inner parts and flattens into a broad (exsag.) facet laterally.

Pygidium. Side view. Axis with only gently convex slope to ring 6, thence falling sharply and terminates overhanging postaxial portion. Axial furrow clear, and postaxial portion weakly concave. Height of pleural lobes more than half total height of ring. Rings very prominent with furrows of about equal strength giving a corrugated outline. Anterior rings vertical, those posteriorly becoming increasingly inclined, reaching 60° to horizontal.

Rear view. Outline of axis semi-octagonal. Inner parts of pleural lobes almost flat, then curving over strongly and falling very steeply. Border convex with concave curve to pleural lobes.

Plan. Outline subsemicircular, with length of axis rather greater than breadth of axis plus one pleural lobe. Axis with almost straight sides tapering to blunt rounded termination.

Fifteen rings which are even bands not narrowing towards axial furrows. Ring 1



TEXT-FIG. 2. Outline reconstruction of the ventral surface of the exoskeleton of *Australosutura gardneri* (Mitchell 1922). Rostrum stippled.

rather narrower than ring 2, and furrow between these two rings longer (sag.) than second furrow. Anterior rings each bear nine to eleven tubercles arranged in somewhat irregular rows. Median row of tubercles, and lateral row of tubercles situated at rather less than half distance from median line to axial furrow larger than the rest giving the semioctagonal outline. A further three to four rows of smaller tubercles; one between median and lateral rows.

Nine ribs, plus three axially arranged rows of tubercles posterior to the axis. Ribs with sharp posterior bend half-way to margin. Anterior portions of ribs twice as strongly arched as posterior portions, and with prominent tubercles, five to eight on ribs 1-8. The tubercles at or near the fulcral angle and the tubercles between the fulcral angle and the axial furrow are more prominent than the others. On rib 5 and posterior ribs the anterior portion does not extend up to the axial furrow and the posterior portion swings diagonally forward across the anterior portion and between it and the axis. Anterior portions of ribs 1-3 join with axial rings so that the junction of the rings and ribs is strongly undulating. The anterior portion of rib 4 scarcely joins the axis and posterior ribs do not do so, so that posterior to rib 4 there is a clear axial furrow which is almost nonundulose. Posterior portions show clearly on ribs 1-6 and narrow to border but do not continue over border except on ribs 1-2. Posterior portions with only one to two tubercles at about half-length (tr.). Border not separated from pleural lobes by any distinct furrow. Border smooth and only slightly undulose but extensions of anterior portions of ribs clear over border and ribs 1-9 with prominent tubercles at margin. Pleural furrows strong and deep, whereas rib furrows clear but weak, deepening at change in slope preceding border. Doublure on pygidium gently convex under border, but inside this it sweeps up steeply. It bears about ten fine raised terrace lines.

Measurements (in mm.)

	<i>Argentina</i>		<i>Australia</i>			
	<i>Brit. Mus. In 53675</i>	<i>Coll. Suero 5049, 5051</i>				
Length of exoskeleton	36.0	..	14.0	(12.0)	..	(17.0)
Breadth of exoskeleton between genal spines	20.0	..	7.5	8.3	..	..
Length of cephalon (sag.)	11.5	..	(5.7)	6.2	4.2	..
Length of glabella	9.0	..	..	..	..	..
Breadth of glabella	8.0	..	5.1	(5.0)	(3.0)	6.2
Breadth of occipital ring (trans.)	7.8	..	..	..	..	..
Length of pygidium	12.5	5.5	..	..	..	..
Length of axis	11.0	4.9	..	..	..	..
Breadth of pygidium	(16.0)	(8.0)	..	..	..	..
Breadth of axis	7.0	3.0	..	..	..	..

Comparisons with Australian material. The Australian specimens are all much smaller than those from Argentina, and in general they are not so well preserved. Further, the only external moulds of the thorax yet discovered are very fragmentary, and most of the external moulds of the cephalon are poorly preserved.

Mitchell (1922, p. 536) described the borders of the cephalon as 'abnormally wide, concave between the cheeks and the thickened margins, which concave portions are only finely and sparsely tuberculate; both inner and outer margins are granulate'. On none

of the specimens we have examined is there any indication of tuberculation on the concave border, and the region is invariably pitted. Mitchell did not mention the glabellar furrows 2p, but these are evident on all specimens, though much less distinctly impressed on the internal surface than in the Argentine specimens.

In general the topotypes do not have such a strongly inflated cephalon as do the Argentine specimens; the glabella does not form a quadrant in side view, but is much more depressed; the glabella does not approach quite so close to the border furrow; the tuberculation of the anterior and lateral border is much weaker and no tubercles have been observed on the posterior border of the fixed cheeks; the tubercles on the glabella are not weaker than elsewhere on the cephalon in well-preserved specimens; no occipital node or other occipital tuberculation has been observed, though this may be due to poor preservation; the crest of the axis of the pygidium does not drop so rapidly behind the sixth ring, and the concentric ornament of the doublure is coarser.

No specimens have been found showing a rostrum, but the course of the ventral margin of the free cheek suggests that the rostrum was similar to the Argentina form.

Repository of material. From Argentina. Museo la Plata, Buenos Aires, Colección Suero: (1) La Carlota, 5048-54, (2) Cerro Mina 5018-46. British Museum (Natural History), London: (1) La Carlota In 53676, (2) Sierra de Tepuel In 53675.

From Australia. Australian Museum, Sydney: Lake Boolambayt, lectotype F.26974, F.26476, F.27345, F.27949, F.44640. Specimens from the two other localities, in Campbell's collection, have been involved in a fire.

K. S. W. C. and R. G.

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A CLYMENIID FROM THE *WOCKLUMERIA* ZONE OF NEW SOUTH WALES

by J. W. PICKETT

ABSTRACT. A new species of clymeniid, *Cymaclymenia borahensis*, from the *Wocklumeria* zone of New South Wales, is described, and its stratigraphical significance discussed. This is the first clymeniid described from Eastern Australia.

IN north-eastern New South Wales, Upper Devonian and Lower Carboniferous rocks consist of a series of geosynclinal sediments, chiefly mudstones, which outcrop in a trough along the western edge of the area, and in a few places along the coast, north of Newcastle. On the western side of the western trough marine faunas of Lower Carboniferous age are well known, but to the east of this trough, in a deeper water environment, fossils are rare. Consequently, any fossils which provide bases for accurate correlation, both within the area and with overseas sequences, are extremely valuable. It has never been possible to define the Devonian-Carboniferous boundary in this sequence, due chiefly to the lack of Devonian marine faunas.

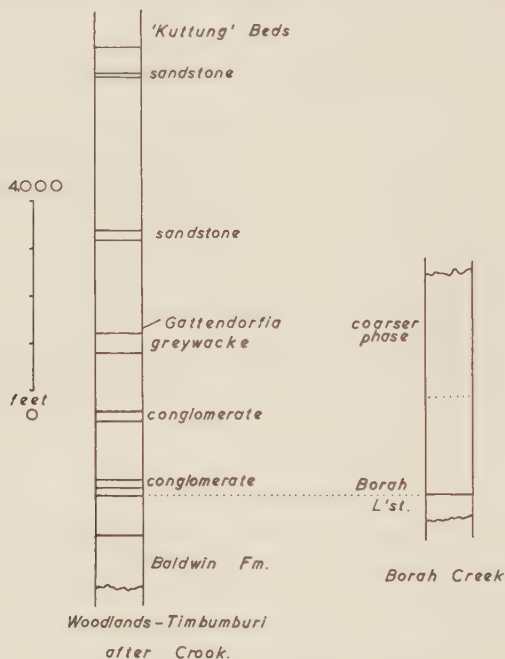
STRATIGRAPHY

The Borah Limestone, in the type locality, is in an incomplete section, but farther south, where it contains fossils only rarely, it can be located in a complete sequence examined by Dr. K. A. W. Crook. Beneath the limestone at the type locality is little more than 50 feet of banded mudstone, with abundant *Leptophloeum australe*. This is absent from the mudstones which overlie the limestone. These mudstones are 200 feet thick and pass up into a coarser phase, in which fine arenites showing graded bedding are the dominant lithological types. This sequence is then truncated by a fault, so that the only known fossil horizons in the sequence are the limestone itself, and the *Leptophloeum* beds. The nature of the limestone is so distinctive that correlation from this locality farther south is quite positive. It is a fine-grained, blue-grey limestone, weathering whitish, containing recrystallized radiolarian tests, and euhedral crystals of an unknown mineral, which has been replaced by a mosaic of albite and calcite. These pseudomorphs, which occur in bands, and are whitish, in contrast to the blue-grey of the limestone, make it an extremely distinctive rock. The outcrop extends for almost 50 miles south-south-east from the type locality, which is the most northerly known outcrop.

This section includes rocks which would belong to the 'Barraba Series' in the lower part, and 'Burindi Series' (of Browne 1950) in the upper part, but it is impossible to make a division, as the boundary of these two has never been defined in a continuous sequence on the eastern side of the trough. The terminology of this interval is at present under review.

Crook's section, in the south, runs in a conformable sequence from low in the Upper Devonian to the Middle Carboniferous. Above the generally unfossiliferous Baldwin Formation is a thick sequence of marine mudstones, with members of limestone, con-

glomerate, greywacke, and sandstone. Some 800 feet above the top of the Baldwin Formation is a limestone with which the Borah Limestone has been correlated. Here, as in the type section, *L. australe* occurs below the limestone, and is not known above it. The *Leptophloeum* extends down into the Baldwin Formation, but is most abundant beneath the limestone. A few feet above the greywacke member (see text-fig. 1) Crook reports a specimen of *Gattendorfia*, which has been identified tentatively, by Crook, as



TEXT-FIG. 1. Stratigraphical columns.

G. minusculum Miller and Collinson, but as the specimen has since been destroyed by a fire this cannot be checked. In America this species occurs in the Northview Shale, of approximately Middle Tournaisian age. Indirectly, through the Northview Shale, this could be correlated with a fauna containing *Protocanites lyoni* (Meek and Worthen), on the western side of the trough in this area.

Above 11,000 feet of these marine mudstones a series of terrestrial, volcanic, and glacial sediments is developed, the 'Kuttung Series' of Browne. It contains plant fossils in places, chiefly *Rhacopteris*. The Tournaisian-Viséan boundary is probably very near this transition from marine to terrestrial sedimentation.

In Catong Gully, north of Somerton, a goniatite which appears to be *Platyclymenia* was collected with specimens of *Leptophloeum australe*. This specimen shows one doubtful suture, and it proved impossible to develop any. The coiling and ornament are quite like that of *Platyclymenia* (see Pl. 41, fig. 7). Unfortunately, the higher part of this section is covered by high-level gravels associated with an earlier stage in the history of the Peel River; as well as this, faulting prevents extrapolation along the strike, so that the relation of this occurrence of *Platyclymenia* to the limestone cannot be determined.

There would be at least 300 feet of sediment between this and the overlying Borah Limestone.

SYSTEMATIC PALAEOONTOLOGY

Genus CYMACLYMENIA Hyatt 1884

Cymaclymenia borahensis sp. nov.

Plate 41, figs. 1-6.

Holotype. Specimen No. F4599, University of New England collections. *Paratypes*. Specimens No. F4600, F4602, University of New England collections. All specimens from type locality (L200, U.N.E. catalogue) on south bank of Borah Creek.

Description. The conch is moderately involute, less so in younger whorls, and platyconic. The whorl height increases markedly in later volution. The maximum number of

TEXT-FIG. 2. Suture of *Cymaclymenia borahensis* sp. nov.

whorls probably does not exceed six. The largest specimen has a maximum diameter of 5.5 cm., and the smallest does not exceed 1 cm., although four whorls are developed. Decoration consists of growth-lines only, fine lirae parallel to the aperture, with a fairly deep, smooth sinus across the venter, and a pronounced ventro-lateral salient. No radial ribs are present. The whorl profile changes during growth, and at maturity is rather similar to that of *C. striata*. The outer whorl is higher than the inner whorls, with tapering sides, and is much less involute. On a mature test, the height of the last whorl is slightly less than half the total conch height.

The suture has a very broad ventral lobe, with a broad, shallow, secondary ventral saddle. The first lateral saddle is well developed, rounded, and the lateral lobe is strongly asymmetrical, with an inflected point on the ventral side. The second lateral saddle is flat, gradually receding into the shallow umbilical lobe, divided by the umbilical seam.

Discussion. *C. borahensis* is more like *C. barbarae* (Loewinson-Lessing) than any of the other species, particularly in regard to the suture. However, Loewinson-Lessing's stratigraphy in the original work is not completely clear. He did not collect the specimens himself, and although he places the fauna in the 'zone of *Sporadoceras münsteri*', it is possible that at least two zones are represented. The only completely reliable report of *C. barbarae* is that of Schindewolf (1952) from Saalfeld, from the *Wocklumeria* zone. The suture of *C. borahensis* is even closer to this than to that of Loewinson-Lessing's specimens.

The two other described species without radial ribs differ from *C. borahensis*, mainly in the degree of development of the first lateral saddle. *C. striata* has a rather similar whorl profile, but the lateral salients are less well developed. *C. camerata* differs in the

whorl profile, though the suture is less different. These two species both occur in the *Clymenia* and *Wocklumeria* zones, so that this, together with the similarity to *C. barbarae*, suggests that *C. borahensis* belongs most likely to the *Wocklumeria* zone.

	<i>Platyclymenia</i>	<i>Clymenia</i>	<i>Wocklumeria</i>
<i>C. striata</i> (Münster)		✓	✓
<i>C. costata</i> (Wedekind)	×	✓	
<i>C. evoluta</i> (Phillips)		✓	✓
<i>C. ornata</i> (Münster)		✓	
<i>C. barbarae</i> (Loewinson-Lessing)	?	✓	✓
<i>C. cordata</i> Wedekind		✓	
<i>C. camerata</i> Schindewolf		✓	✓
<i>C. ovata</i> Schindewolf		✓	
<i>C. borahensis</i> sp. nov.			✓
<i>C. dorsocostata</i> (Münster)		?	

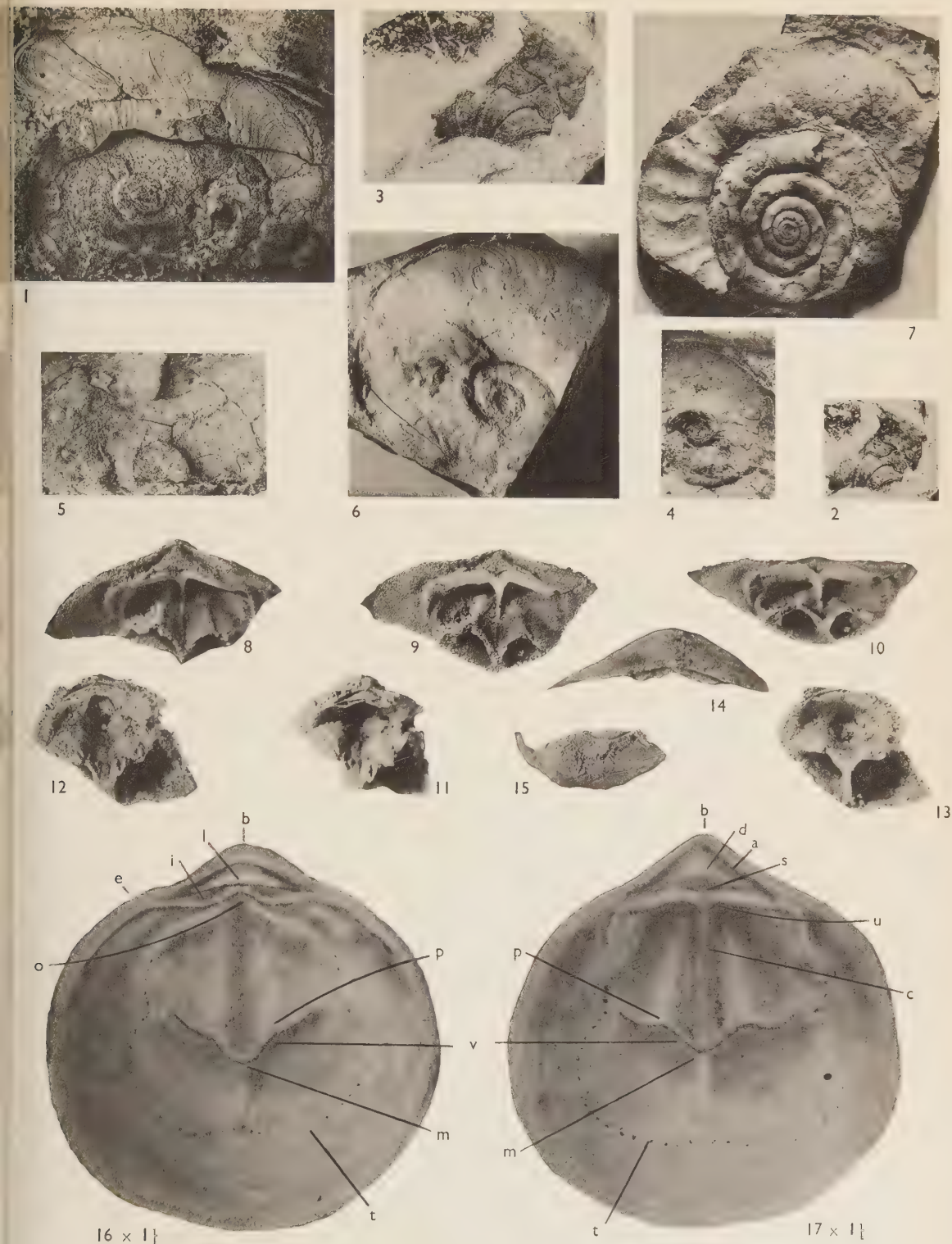
Ranges of *Cymaclymenia* species.

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EXPLANATION OF PLATE 41

- Figs. 1–6. *Cymaclymenia borahensis* sp. nov., Borah Limestone, Borah Creek. 1, Paratype, F4600, showing aperture and growth lines, $\times 1$. 2, 3, Holotype, F4599, showing sutures; 2, $\times 1$; 3, enlarged. 4, Sutures and part of living chamber, F4601, $\times 1$. 5, Youngest suture and part of living chamber, F4603, $\times 1$. 6, Paratype, F4602, showing umbilicus, growth lines, and part of living chamber, $\times 1$.
- Fig. 7. ?*Platyclymenia* sp., Upper Catong Gully, Attunga; F4618, $\times 1$.
- Figs. 8–17. *Dinobolus* sp. cf. *D. conradi* (Hall), Sandpile group, British Columbia. 8–15 are unretouched photographs, $\times 1$; 16, 17 are drawings illustrating the terminology, $\times 1\frac{1}{2}$. 8, 11, Internal views of the incomplete pedicle and brachial valves, Geol. Surv. Canada 14487. 9, 10, 12, 13, Internal views of the same valves tilted; 9, 10, pedicle valves, 12, 13, brachial valves. 14, 15, Posterior views of the pedicle and brachial valves. 16, 17, Reconstructions of the complete brachial and pedicle valves (outlines and anterior parts adapted from Davidson and King 1874). *a*, groove; *b*, beak; *c*, cardinal buttress; *d*, pseudodeltidium; *e*, cardinal partition; *i*, cardinal impression; *l*, plate; *m*, median partition; *o*, subcardinal impression; *p*, platform; *s*, cardinal socket; *u*, umbonal chamber; *v*, platform vault; *t*, position of trace of anterior part of crescent.



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A WELL-PRESERVED *DINOBOLUS* FROM THE SANDPILE GROUP (MIDDLE SILURIAN) OF NORTHERN BRITISH COLUMBIA

by B. S. NORFORD

ABSTRACT. A silicified individual allows a more detailed description of the posterior portion of *Dinobolus* than was previously available. There is no trace of the existence of a pedicle and a functional pedicle may have been atrophied in the genus.

THE Sandpile group (Middle Silurian) of northern British Columbia contains an extensive silicified coral and brachiopod fauna preserved in fine-grained, slightly cherty, thick-bedded dolostones. A single incomplete specimen of *Dinobolus* was etched free and is thought to represent a mature individual. The two valves were in contact within the rock, but became separated during the etching process.

In the descriptions of the genus and of the family by Hall and Clarke (1892), and by Davidson and King (1874), the internal characters are almost entirely based on naturally forming internal moulds, whereas the Sandpile specimens are silicified valves. The Schuchert Collection at Yale University contains a representative selection of the Trimerellidae including gutta-percha impressions taken from many of the internal moulds from which Hall and Clarke reconstructed drawings of the original valves (Hall and Clarke 1892, pl. 4A-4D). In most of these drawings the beak and hinge regions of the valves have been considerably restored.

The Sandpile material does not amplify knowledge of the interiors of the valves over that presented by Davidson and King, but does allow further description of the structures of the hinge, and of the pseudodeltidium. Most of the terminology is derived from Davidson and King (1874), but the following terms are also used in this discussion for convenience of description: cardinal socket, pseudodeltidium, plate (Pl. 41, figs. 16, 17).

Family TRIMERELLIDAE Davidson and King 1874

Genus DINOBOLUS Hall 1874

Type species *Obolus conradi* Hall 1868

Dinobolus sp. cf. *D. conradi* (Hall)

Plate 41, figs. 8-17

?*Obolus conradi* Hall 1868, pp. 368-9.

?*Dinobolus conradi* (Hall); Davidson and King 1874, pp. 160-1.

?*Dinobolus conradi* (Hall); Hall and Clarke 1892, pp. 38-39.

Description. Test biconvex, thick shelled, with faint concentric growth-lines near the margin. Pedicle valve with a small beak. Pseudodeltidium low, broadly triangular, slightly convex, bounded laterally by two grooves, and with a well-developed anterior slope curving into the cardinal socket at the hinge; without ornament preserved on the surface of the pseudodeltidium and without perforation or median groove (Pl. 41,

figs. 8, 9). Hinge plate bearing a low pedically directed undulation and supported by a well-developed cardinal buttress (*c* of fig. 10). Platform prominently vaulted with a biconvex brachial surface, vaults separated by a median partition (*m*). Cardinal buttress forming a double-chambered umbonal cavity; buttress tapered anteriorly, resting medially on the platform. Muscle scars present on the platform and on the valve floor outside it.

Brachial valve with an inconspicuous beak. A thin, elevated, saucer-like, transverse plate located in front of the beak and fitting snugly into the cardinal socket of the pedicle valve (fig. 15). Two cardinal impressions on the hinge immediately in front of this plate, moulding the brachial surface of the pedicle valve's hinge plate. Platform vaulted, with a depression above the median partition, surface biconvex but less strongly so than the surface of the platform of the pedicle valve. Umbonal cavity with a deep subcardinal impression (the figured specimen shows a hole in the shell at the centre of this depression).

Distribution. Sandpile group, Geological Survey of Canada collection 35165, from altitude 5,750 feet, 2 miles north-west of the southerly of the two lakes in Sandpile Creek, McDame, British Columbia; 59° 03' north, 128° 11' west. Geological Survey of Canada numbers 14487*a* (pedicle valve) and 14487*b* (brachial valve).

Discussion. The paucity of the studied material and the lack of complete valves preclude a complete description and identification, but the individual agrees with *Dinobolus conradi* (Hall) as discussed by Hall and Clarke who allowed a great deal of variation within the species. *D. conradi* has been reported from rocks of Niagaran age.

Davidson and King (1874) described one structure that they thought characterized the Trimerellidae, the sub-marginal crescent, confined to the posterior half of each valve and formed of three portions, the crown, the sides, and the ends. 'This part (p. 130), or merely a portion of it, may present itself in relief, excavated, obscurely, often partially in any of these conditions, or complicated by successive enlargements of its area; so that we feel a difficulty in representing it otherwise than diagrammatically, or in giving a description that is strictly accurate when applied to any single case.'

The crown is described as a line, the sides as pointed ovals, and the ends as obscurely defined areas. Examination of the specimens from British Columbia finds the crown to be situated between the hinge and the pseudodeltidium, i.e. at the site of the cardinal socket, and it appears to have little in common with the sides of the crescent, other than geometric continuity. The sides and ends of the crescent may well be the sites of muscle scars.

The cardinal facet of Davidson and King (p. 128, corresponding to the cardinal socket of this description) 'generally inclines or falls towards the cavity of the shell', and (p. 130) 'there is situated on the cardinal facet an oval-shaped scar or *lozenge* (*g*), having its long axis in the transverse direction of the valve'. This socket houses the plate of the brachial valve when the valves are in contact.

The deltidium of Davidson and King (pseudodeltidium of this description) represents the track on the pedicle valve of the edge of the plate of the brachial valve, and its anterior slope (deltidial slope of Davidson and King) suggests accelerating increase in size of the plate and the cardinal socket during growth.

The grooves bordering the pseudodeltidium are thought to represent the tracks of the cardinal extremities of the brachial valve. No trace was observed of 'deltidial ridges'.

Discussing the brachial valve, Davidson and King state (p. 128): 'The central portion of the hinge in certain species show nothing remarkable, . . . but in others it distinctly displays an excavation or *cardinal scar* . . . the excavation is biccupped in *T. ohioensis*: but the same species also presents it transversely grooved. There is no prominence in these cases. In some other species, however, the cardinal scar, though in general badly seen, appears to be situated on an elevation . . . rounded, or squared, and more or less developed, according to species. Nay, in the same species, as in *T. Lindströmi*, the elevation varies much in size, certain individuals having it very small, others very large and standing out like a great tooth . . . so large that it must have dipped deeply into the umbonal cavity of the pedicle-valve.'

Comparing these statements with the Sandpile specimens, and bearing in mind the nature of the internal moulds from which the authors drew most of their information, their elevation corresponds to the plate, which lies immediately behind the pair of cardinal impressions, referred to by them as the cardinal scar. This explanation suggests that their material revealed these structures so poorly that confusion of such closely adjacent structures was possible.

Investigation of *D. sp. cf. D. conradi* reveals no trace of a pedicle opening in the pseudodeltidium, nor of a groove in the hinge region of either valve, such as might be expected had the pedicle passed between the valves. Indeed, the plate of the brachial valve fits into the cardinal socket and would prevent the extrusion of a median pedicle. A functional pedicle may have been completely atrophied in *Dinobolus* and possibly also in the rest of the Trimerellidae.

There is no trace of the hinge teeth and sockets that characterize the class Articulata, but the species certainly does possess articulation as defined by Schuchert and Cooper (1932, p. 6), thus leaving as obscure the position of the Trimerellidae in a scheme of classification.

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